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The causes and consequences of social and genetic structure in the monk parakeet, *Myiopsitta monachus*

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General summary

The genetic and social structure of populations has considerable ecological, behavioural, and evolutionary implications and may arise from various demographic traits. In this thesis, I combine field observations and molecular genetic techniques to explore the causes and consequences of both the genetic and social structure of the monk parakeet, *Myiopsitta monachus*. This unusual parrot species is highly social, living in colonies and often building compound nests with multiple individual nest chambers. First, I developed new microsatellite markers for the monk parakeet that I then used for all subsequent work. Using spatial autocorrelation analyses of pairwise genetic relatedness, I then revealed that relatives are spatially clustered within shared compound nests and nesting trees. This pattern is driven by several demographic processes, including limited and coordinated dispersal and high site fidelity. Next, I investigated habitat preferences of birds following natal dispersal to their first breeding attempt, showing that habitat choices are at least partly driven by experience in the natal habitat, termed natal habitat preference induction. Moreover, the habitat preferences of adults were also maintained through breeding dispersal movements. I then describe the monk parakeet breeding system in detail, revealing that while the majority of breeding attempts were made by pairs, approximately 20% of attempts were made by groups, with marked flexibility in group size, sex-ratio, ages and genetic relatedness of group members. Multiple members of groups may achieve parentage in a single brood, and in pairs some extra-pair paternity was detected. Finally, I show that despite relatives being clustered in compound nests and nesting trees, social associations between individuals when away from the nest are associated with nest proximity rather than kinship. These results add to our understanding of the factors driving dispersal decisions and their consequences for social evolution, with diverse implications for applied and fundamental ecology.

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Declaration

I, Francesca Dawson Pell, confirm that the Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (www.sheffield.ac.uk/ssid/unfair-means). This work has not been previously presented for an award at this, or any other, university.

Publications

Data chapters 2 and 3 are published in *Molecular Biology Reports* and *Molecular Ecology* respectively, and appear with only minor formatting edits in this thesis. Full references:

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1. General introduction

This thesis addresses questions pertinent to both fundamental and applied ecology, and to the evolution of social and cooperative behaviour using an unusual social parrot species: the monk parakeet, *Myiopsitta monachus*. In this chapter, I will present relevant contextual information on dispersal, group living and social systems. I then discuss parrot social and breeding systems and introduce the study species and site in detail. Finally, I provide an outline of the scope of the thesis by chapter and provide details of contributions to this thesis.

1.1 Dispersal and population structure

1.1.1 Dispersal

Dispersal is a key life-history process with diverse ecological and evolutionary implications. Dispersal is defined as the movement of an individual from one area to another and is often considered to involve three stages: first, emigration from the natal or breeding location, second, a period of transience as an individual moves through the landscape, and third, immigration into the new site for settlement (Clobert, Danchin, Dhondt, & Nichols, 2001; Bowler & Benton, 2005). Dispersal can take place at various life stages and occur more than once across an individual's lifespan; natal dispersal is defined as the first movements of an individual from its natal area to a new area potentially suitable for reproduction, and breeding dispersal is the movements of an individual between consecutive breeding sites (Howard, 1960; Clobert et al., 2001). The influences of dispersal are apparent at the level of the gene, individual and population, therefore dispersal is a key determinant of gene flow, population dynamics, and resulting population genetic structure (Broquet & Petit, 2009). Furthermore, dispersal facilitates range expansions, the colonisation of new areas, and may enable species to respond adaptively to changes in their environment (Kokko & López-Sepulcre, 2006; Duckworth & Badyaev, 2007; Broquet & Petit, 2009).

Studies into the drivers of dispersal have resulted in hypotheses regarding both proximate and ultimate causes of observed dispersal patterns (e.g. Ferreras et al., 2004; Long, Diefenbach, Rosenberry, & Wallingford, 2008). Among the ultimate causes of individual dispersal are: inbreeding avoidance, resource competition and mate competition (Greenwood, 1980; Perrin & Mazalov, 2000; Costello, Creel, Kalinowski, Vu, & Quigley, 2008; Szulkin & Sheldon, 2008), whereas proximate mechanisms thought to influence dispersal decisions include ontogenetic (e.g. Holekamp, 1986), ecological (Pasinelli & Walters, 2002) and social factors (Christian, 1970; Bekoff, 1977). Multiple mechanisms may interact to influence dispersal decisions within a species and the importance of each driver can vary between and within populations and even between individuals (Serrano, Tella, Donázar, & Pomarol, 2003).

Among the proximate mechanisms that can influence dispersal behaviour and habitat selection is personal information that is accrued through prior breeding experience (Newton & Marquiss, 1982; Fowler, 2005). For instance, site return rates and patterns of dispersal are linked to nesting failure in American robins, *Turdus migratorius*, and brown thrashers, *Toxostoma rufum* (Haas, 1998), and breeding site fidelity is positively influenced by breeding success in cackling Canada geese, *Branta canadensis minima* (Fowler, 2005). Personal information gathered through early life experience may also influence dispersal behaviour and habitat selection during later life stages. Natal habitat preference induction (NHPI) occurs when animals demonstrate a preference for habitats as adults which exhibit similar environmental cues to those experienced in their natal habitat (Davis & Stamps, 2004; Stamps & Davis, 2006). NHPI is an important influence in the process of habitat selection in a broad range of taxa including: fish (e.g. Arvedlund, McCormick, Fautin, & Bildsøe, 1999), insects (e.g. Lhomme, Carrasco, Larsson, Hansson, & Anderson, 2018), amphibians (e.g. Hepper & Waldman, 1992), mammals (e.g. Haughland & Larsen, 2004; Merrick & Koprowski, 2016) reptiles (e.g. Roe, Frank, Gibson, Attum, & Kingsbury, 2010) and birds (e.g. Piper, Palmer, Banfield, & Meyer, 2013). NHPI has been implicated as a mechanism driving parapatric divergence (Bolnick et al., 2009), increasing reproductive isolation and re-enforcing habitat shifts (Vallin & Qvarnström, 2011) and ultimately influencing patterns of speciation (Beltman & Metz, 2005; Tonnis, Grant, Grant,

& Petren, 2005); it also has implications for conservation practises (Roe et al., 2010; Kleinstäuber, Kirmse, & Langgemach, 2018).

In addition to the personal information available to individuals from either their natal or prior breeding experience, individuals may be able to access social information pertinent to dispersal and habitat selection decisions. Such information can include deliberate signals or unintentional cues from both conspecifics and heterospecifics indicating the suitability of a site (e.g. Danchin, Giraldeau, Valone, & Wagner, 2004; Kivelä et al., 2014). One potential driver of settlement and departure decisions is public information (inadvertent social information) provided by conspecific presence (Farrell, Morrison, Campomizzi, & Wilkins, 2012) and/or breeding success (Kivelä et al., 2014). For instance, blue tits, *Cyanistes caeruleus*, use both fledgling quantity and quality to make breeding site decisions (Parejo, White, Clobert, Dreiss, & Danchin, 2007) and collared flycatchers, *Ficedula albicollis*, use conspecific breeding success from the previous breeding season to select nest sites (Kivelä et al., 2014). However, personal information, for example information gathered about habitat structure, has been shown to be more important than social information in some cases (Berg & Eadie, 2020).

Dispersal can be a risky undertaking. Compared with non-dispersers, individual dispersers may have a higher rate of predation (reviewed in Bonte et al., 2012), risk injury from individuals defending the groups or habitats that dispersers try to integrate into (Grinnell, Packer, & Pusey, 1995), lose a larger amount of body mass (Ridley, 2012) and often suffer a higher risk of mortality (Ferreras et al., 2004). However, such costs of dispersal are not universal (e.g. Long, Diefenbach, Lutz, Wallingford, & Rosenberry, 2021) and employing efficient movement strategies during the transient phase can help to mitigate the energetic costs of large movements (Klarevas-Irby, Wikelski, & Farine, 2021). Dispersing in coalitions of individuals can mitigate some of the costs of lone dispersal; for example, social information may be available from dispersing group members about predators or resources reducing overall dispersal costs for individuals moving through areas of unknown habitat (Krause &

Ruxton, 2002; Yoder, Marschall, & Swanson, 2004; Lee, Lee, & Hatchwell, 2010). Dispersing coalitions may also be more likely to become established in a new group; for instance, compared to single male lions, *Panthera leo*, coalitions of males are more likely to take control of prides, gaining access to more mates and producing higher numbers of offspring (Bygott, Bertram, & Hanby, 1979).

Dispersal coalitions in a number of social mammals and birds involves the joint immigration of relatives (e.g. Packer & Pusey, 1993; Heinsohn, Dunn, Legge, & Double, 2000; Matthysen, Van De Casteele, & Adriaensen, 2005; Hammond, Handley, Winney, Bruford, & Perrin, 2006; Le Galliard, Gundersen, Andreassen, & Stenseth, 2006; Bradley, Doran-Sheehy, & Vigilant, 2007). Dispersing in family groups can prevent the dilution of kin structure that is normally assumed to result from dispersal movements (Sharp, Simeoni, & Hatchwell, 2008; Lee et al., 2010). The resulting spatial aggregation of relatives following dispersal allows the continuation of the various benefits of associating with kin (Clobert, et al., 2001; Sharp et al., 2008; Lee et al., 2010). For instance, in long-tailed tits, *Aegithalos caudatus*, helping behaviour may subsequently be directed towards kin from groups of related immigrants, allowing indirect fitness benefits to be accrued amongst immigrants as well as among philopatric recruits (MacColl & Hatchwell, 2004; Sharp et al., 2008), and in vinous-throated parrotbills, *Paradoxornis webbianus*, breeding near male relatives increases fledgling success (Lee et al., 2010). However, dispersing in coalitions of relatives may also increase the risk of kin competition post-dispersal, as well as incurring a risk of inbreeding if opposite-sex kin are involved (Lee et al., 2010).

Dispersal behaviour is inherently challenging to study in open populations (Koenig, Van Vuren, & Hooge, 1996). Despite much research effort examining the drivers of dispersal and dispersal outcomes, there has been little research into pre-dispersal exploratory or ranging movements by individuals. Such ranging movements may play a role in determining dispersal decisions and patterns and add to our understanding of the process of dispersal as a whole. Juvenile roe deer, *Capreolus capreolus*, readily explore before dispersal (Van Moorter et al., 2008), with dispersal direction correlated with exploration direction, and individuals that dispersed more likely to explore than individuals that remained philopatric (Debeffe et al., 2013). Red-bellied woodpeckers, *Melanerpes carolinus*, have also been shown to make repeated forays from the natal range prior to dispersal (Cox & Kesler, 2012). However, despite these examples of exploratory and ranging movements and the potential links between such behaviours and dispersal movements and decisions, evidence is limited and pre-dispersal movements remain an understudied area of dispersal ecology with many avenues for potential investigation.

1.1.2 Population genetic structure

Patterns of dispersal are critical in determining population genetic structure (the distribution and frequency of alleles and genotypes within and between populations) at a range of spatial scales (Painter, Crozier, Poiani, Robertson, & Clarke, 2000; van Dijk, Covas, Doutrelant, Spottiswoode, & Hatchwell, 2015). Population genetic structure can have diverse ecological, evolutionary and behavioural implications including influencing kin competition (West, Pen, & Griffin, 2002), cooperative behaviour (Leedale, Sharp, Simeoni, Robinson, & Hatchwell, 2018), mate choice (Lee, Simeoni, Burke, & Hatchwell, 2010) and inbreeding risk (Brouwer, van de Pol, Atema, & Cockburn, 2011) at small spatial scales, and patterns of local adaptation and speciation at broad spatial scales (Winker, McCracken, Gibson, & Peters, 2013).

There are numerous factors that can influence population genetic structure, for example, limited dispersal due to geographical distances (isolation by distance), physical barriers such as those created by habitat fragmentation (Ortego, Aguirre, Noguerales, & Cordero, 2015), or other landscape features such as rivers or roads (Wright, 1943; Garnier, Alibert, Audiot, Prieur, & Rasplus, 2004; Hayes & Sewlal, 2004; Riley et al., 2006). Allele distribution and frequency can also be influenced by chance, especially in small populations, by random genetic drift and founder effects (Lacy, 1987; Bai, Ke, Consuegra, Liu, & Li, 2012). Population bottlenecks, i.e. extreme reductions in population size, may also influence population genetic structure through eliminating less frequent alleles and subsequently reducing overall genetic diversity (e.g. Thornton & Andolfatto, 2006).

Fine-scale population genetic structure has been detected among adults following the period of natal dispersal in a number of species, often reflecting patterns of sex-biased dispersal. For instance, female-biased dispersal in the white-breasted thrasher, *Ramphocinclus brachyurus* (Temple, Hoffman, & Amos, 2006), and the sociable weaver, *Philetairus socius* (van Dijk et al., 2014; van Dijk et al., 2015), leads to significant genetic structure amongst the more philopatric males. In contrast, male-biased dispersal in the white-browed sparrow weaver, *Plocepasser mahali* (Harrison, York, & Young, 2014), and the white-throated magpie-jay, *Calocitta formosa* (Berg, Eadie, Langen, & Russell, 2009), leads to stronger within-group genetic structure amongst females. Such sex-biased natal dispersal is a passive mechanism for inbreeding avoidance that may considerably reduce the risk of inbreeding (Johnson & Gaines, 1990). However, despite the capacity for dispersal to dilute kin structure in wild populations there is growing evidence that dispersal in coalitions of relatives can maintain kin structure in individuals that have dispersed from their natal area. For instance, dispersing sibling coalitions have been described in a number of avian species, including the long-tailed tit (Sharp et al., 2008), and the brown jay, *Cyanocorax morio* (Williams & Rabenold, 2005). Dispersal of sibling coalitions can maintain the benefits of associating with kin beyond dispersal and provide opportunities for kin-selected cooperation (Sharp et al., 2008).

In conclusion, demographic processes such as limited or coordinated dispersal can lead to significant population genetic structure within stable social groups (Berg et al., 2009) and also within extended ‘kin neighbourhoods’ (Dickinson & Hatchwell, 2004; Leedale et al., 2018), and sex-biased dispersal can determine patterns of within and between-sex relatedness (Temple et al., 2006; Harrison et al., 2014). The kin-composition of social groups resulting from varying patterns of dispersal determines opportunities for direct and indirect fitness benefits but also may influence conflict and costs within groups (*see below*).

1.2 Group living and sociality

1.2.1 Group living

Many species, across a variety of taxa, live and breed in groups or colonies. Group living can entail costs to individual group members, for example through increased competition over foraging (Radford & Ridley, 2008; Lamb, Satgé, & Jodice, 2017), reproduction (Emlen, 1982; Koenig, Mumme, Stanback, & Pitelka, 1995), mates (Zhao, Ji, Li, & Watanabe, 2008), or breeding locations (Ramos, Monteiro, Sola, & Moniz, 1997) and also increased risk of parasite transmission (Côté & Poulin, 1995; Patterson & Ruckstuhl, 2013). A meta-analysis revealed that the size of animal groups was a weak predictor of the risk of parasitism, unless animals were in large aggregations, such as the aggregations found in colonial birds (Rifkin, Nunn, & Garamszegi, 2012). However, there are contrary suggestions that group living may have anti-parasite benefits though improved host resistance and a reduction in the fitness costs of infection (Ezenwa, Ghai, McKay, & Williams, 2016). An additional cost to reproductive success in colonial animals that rear young in nests can come from conflict over nesting material which can lead to nest material kleptoparasitism, where individuals remove material from another individual's nest for use in their own. For example, stone theft has been observed in a colony of Chinstrap penguins, *Pygoscelis antarctica*, and can influence the chance of a nest being flooded and the subsequent risk of losing offspring (Moreno, Bustamante, & Vifiuela, 1995).

Living in groups or colonies can also bring a variety of benefits to individuals and provide opportunities for cooperation. Group living can reduce the risk of predation through improved predator defence or detection (Hamilton, 1971; Pulliam, 1973). For instance, nests of the common gull, *Larus canus*, are more likely to be depredated if they are solitary compared to within a colony (Götmark & Andersson, 1984). Colony size and density can also influence predation risk (Poiani, 1991; Berg, Lindberg, & Gunnar, 1992); nests in larger colonies of lapwings, *Vanellus vanellus*, are less likely to be predated than nests in smaller colonies (Berg et al., 1992) and detection of a decoy predator increases with increasing colony size in Montagu's harrier, *Circus pygargus* (Arroyo, Mougeot, & Bretagnolle, 2001). Another potential benefit of colony living is communication of information (Ward & Zahavi, 1973), for example, information about resources that can improve foraging efficiency or resource access and quality assessment (e.g. Canonge, Deneubourg, & Sempo, 2011; Donaldson-Matasci, DeGrandi-Hoffman, & Dornhaus, 2013). In some species, the size of the colony determines the effectiveness of information gathering, for example, larger colonies of Italian honeybees, *Apis mellifera ligustica*, are able to locate and recruit individuals to resource patches quicker than smaller colonies (Donaldson-Matasci et al., 2013). Living in groups also provides opportunities for cooperation during breeding (*see below*).

1.2.2 Cooperative breeding

In cooperatively breeding species, more than two individuals engage in parent-like behaviour to raise young from a single brood or nest (Emlen, 1991; Hatchwell & Komdeur, 2000). Such parental behaviour (often referred to as helping when involving non-breeding individuals) can involve a variety of behaviours including: babysitting young (Clutton-Brock et al., 1998), territory maintenance activities and defence (Taborsky, 1984; Josi, Freudiger, Taborsky, & Frommen, 2020; Josi, Taborsky, & Frommen, 2020), allofeeding incubating adults and provisioning young (Lloyd, Taylor, Du Plessis, & Martin, 2009). Cooperative breeding is relatively uncommon, being recorded in only 3% of mammal species, 9% of bird species (Emlen, 1991; Cockburn, 2006) and less than 0.1% of fish (Taborsky, 1994), although the phenomenon is likely under-reported, particularly in birds, due to a lack of information from certain continents (Cockburn, 2006).

Cooperative breeding behaviour differs between species, and amongst vertebrates breeding in a group can be obligate (e.g. white-winged chough, *Corcorax melanorhamphos* (Heinsohn, Cockburn, & Cunningham, 1988); and chestnut-crowned babbler, *Pomatostomus ruficeps* (Russell, Portelli, Russell, & Barclay, 2010)), or more commonly, facultative (e.g. long-tailed tit (Russell & Hatchwell, 2001)). Cooperative groups also vary in their size, sex-ratio and structure; additional individuals may be offspring that have delayed dispersal (Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992), immigrants to the territory (Baglione, Canestrari, Marcos, & Ekman, 2003), failed breeders (MacColl & Hatchwell, 2002) or a mix of these (Preston, Briskie, Burke, & Hatchwell, 2013). In addition, helping behaviours can be directed towards kin or non-kin (review: Hatchwell, 2009; Riehl, 2013), and the kin composition of cooperative groups determines the opportunities for indirect fitness benefits of raising non-descendant kin and assisting related breeders (*see below*; Hamilton, 1964). There are also numerous systems which involve variations of plural breeding or cooperative polygamy in which more than one male or female participates in breeding within a group (e.g. Barve et al., 2021; Marshall et al. 2021). For example, eclectus parrots, *Eclectus roratus*, have a breeding system that involves cooperative polyandry with up to seven males to a single breeding female reported (Heinsohn, Ebert, Legge, & Peakall, 2007).

Helping behaviour can come at a price, with costs varying depending on the particular behaviours involved (reviewed in Heinsohn & Legge, 1999). Significant energetic investment, which may result from activities such as territory and predator defence, can lead to helpers growing at a slower rate than non-helpers (Taborsky, 1984). Helpers may also forgo foraging for extended periods with significant energetic costs, for example in the meerkat, *Suricata suricatta*, helpers babysit pups and are unable to feed for 24 hours (Clutton-Brock et al., 1998). Babysitters that contributed most over the breeding period lost 3.8% of their body weight on average, indicating high energetic costs can be associated with helping behaviour (Clutton-Brock et al., 1998). Costs may also be long-lasting, extending beyond the breeding season and can include higher mortality rates, for instance helpers in stripe-backed wrens, *Campylorhynchus nuchalis*, that provision young at higher rates have reduced survival (Rabenold, 1990). In groups with co-breeding individuals, there may also be reproductive conflict over who produces offspring when a clutch or brood may have a size limit that results in reduced per capita offspring numbers (Koenig, 1981). Such conflict can lead to group members killing offspring (Kutsukake & Clutton-Brock, 2006) or destroying the eggs of co-breeders (Koenig et al., 1995). There are also avenues for conflict over investment in cooperative groups, which can lead to ‘punishment’ for group members that do not contribute (Naef & Taborsky, 2020). Finally, there may also be foraging competition between group members that forage together, for example, in green woodhoopoes, *Phoeniculus purpureus*, dominant group members monopolise the richest foraging niches, excluding subordinates (Radford & Du Plessis, 2003).

There has been much research interest in the benefits of additional group members or helpers (e.g. Cockburn, 1998; Dickinson & Hatchwell, 2004). There is evidence that helpers can increase: nestling or fledgling condition and body mass (te Marvelde, McDonald, Kazem, & Wright, 2009; Bolopo, Lowney, & Thomson, 2019), juvenile survival (McGowan et al., 2003), and the overall probability of successful reproduction (Josi et al., 2020). Additional group members may also reduce reproductive costs for breeders (Hatchwell, 1999) and delay breeder senescence (Hammers et al., 2019). Benefits to the offspring receiving care from helpers have also been shown to occur over both short and long timescales, indicating the potential for long-term benefits to helper presence (Hodge, 2005; Brouwer, Richardson, & Komdeur, 2012). However, benefits to having helpers are not always found, for example, helpers do not increase either survival or reproductive success in the white-browed scrubwren, *Sericornis frontalis* (Magrath & Yezerinac, 1997). There are several reasons why benefits of helper presence may not be detected. It has been suggested when helpers are not found to provide any benefits it may be the result of study design rather than an absence of help (Downing, Griffin, & Cornwallis, 2020), that the benefits of helpers may be apparent only under adverse breeding conditions (Covas, Du Plessis, & Doutrelant, 2008), or that differences in maternal egg-investment could conceal the effects of the helpers (Russell, Langmore, Cockburn, Astheimer, & Kilner, 2007). The quality of the individuals helping can also impact reproductive success, for example, in the El Oro parakeet, *Pyrrhura orcesi*, both clutch sizes and fledging success were increased by the quality of helpers (Klauke, Segelbacher, & Schaefer, 2013).

Helping can also provide a variety of direct fitness benefits to the helper or additional group members (Cockburn, 1998; Dickinson & Hatchwell, 2004) that can be derived by the helper at the time of helping, or in the future (Woolfenden & Fitzpatrick, 1978; Richardson, Burke, & Komdeur, 2002). Direct benefits that can arise during the period of helping include: a lower risk of mortality due to protection by other group members or shelter in the shared territory (Taborsky, 1984; Taborsky, 1985), access to breeding opportunities within their group (Emlen, 1996; Richardson et al., 2002), and further reproductive opportunities beyond the group via extra-pair copulations (Mulder, Dunn, Cockburn, Lazenby-Cohen, & Howell, 1994). There are also potential future benefits of helping that are realised after the helping period and may include: future breeding territory acquisition through budding or inheritance (Woolfenden & Fitzpatrick, 1978; Temple, Hoffman, & Amos, 2009) and increased reproductive success resulting from previous breeding experience whilst helping (Heinsohn et al., 1988; Komdeur, 1996).

Kin selection (selection for traits due to their beneficial effects on the fitness of related individuals) is vital in our understanding of the inclusive fitness benefits derived from helping behaviour (Hamilton, 1964). The kin-selected benefits of helping are derived from increased production of non-descendant kin; resulting in an increase in the indirect component of an individual’s inclusive fitness (reviewed in Cockburn, 1998). For example, helpers in western bluebirds, *Sialia mexicana*, increase both the growth rate of nestlings and their subsequent chance of successfully fledging, resulting in indirect fitness benefits for helpers (Dickinson, Koenig, & Pitelka, 1996), and helpers in the long-tailed tit gain indirect fitness benefits through the increased survival of related offspring and breeders by helping at the nests of kin (Hatchwell, Gullett, & Adams, 2014). Both direct and indirect fitness benefits may be derived by helpers in one helping system and the various benefits may influence different aspects of helping behaviour (Dickinson, 2004). For instance, indirect benefits influenced whether potential western bluebird helpers actually engage in helping activities, but current direct fitness benefits influenced the rate of food delivery to nestlings (Dickinson et al. 1996; Dickinson 2004).

When relatedness in groups is variable or when species live in extended ‘kin neighbourhoods’ and average genetic relatedness tends to be low, mechanisms of kin discrimination that enable individuals to reliably direct their care towards relatives may be selected for (Cornwallis, West, & Griffin, 2009). For instance, vocal cues correlate with kinship in the long-tailed tit, and helpers assist breeders with calls more similar to their own vocalisations (Leedale, Lachlan, Robinson, & Hatchwell, 2020). Such mechanisms of kin discrimination may also play an important role in reducing the risk of inbreeding, particularly when individuals live in close proximity with kin and passive processes, such as dispersal of one sex, does not prevent interactions with kin (Pusey & Wolf, 1996; Leedale et al., 2020).

1.2.3 Social associations

In many species, social interactions and associations within groups or populations are non-random (e.g. Whitehead, 2008; Kurvers et al., 2013). Choices made by individuals regarding their social associates can have wide-ranging implications for a multitude of evolutionary and ecological processes; social associations can determine pair formation and mating patterns (Oh & Badyaev, 2010), foraging behaviour (Firth, Voelkl, Farine, & Sheldon, 2015) and survival (Stanton & Mann, 2012). Social bonds can also bring additional fitness benefits such as higher fledging success (Riehl & Strong, 2018) and improved offspring survival (Frère et al., 2010). In addition, social associations and network structure can also impact disease and parasite transmission between individuals (Hamede, Bashford, McCallum, & Jones, 2009; Sah, Leu, Cross, Hudson, & Bansal, 2017; Sah, Mann, & Bansal, 2018), the transmission of information through a population (Firth, Sheldon, & Farine, 2016), and have been shown to determine patterns in gut microbiomes (Perofsky, Ancel Meyers, Abondano, Di Fiore, & Lewis, 2021).

Social network analysis is increasingly being used to describe and quantify social dynamics, the structure of populations and to investigate the factors underlying social associations (e.g. Whitehead, 2008; Best, Dwyer, Seddon, & Goldizen, 2014; Diaz-Aguirre, Parra, Passadore, & Möller, 2019). Social network analysis provides a snapshot of social connections between individuals in a population and is a powerful toolkit to accurately portray social groups in a comparable and quantitative way, thus allowing robust testing of a wide range of hypotheses (Croft, James, & Krause, 2008; Farine & Whitehead, 2015; Krause, James, Franks, & Croft, 2015).

Factors underlying social structure can be many and varied and include kinship (Gaspari et al. 2007), familiarity (Best et al., 2014), foraging strategies (Methion & Díaz López, 2020), age (Chiyo et al., 2011), sex (Rimbach et al., 2015; Silk et al., 2018), and the inheritance of social associates from parents (Ilany & Akçay, 2016). Gaining a better understanding of the factors that underlie animal social structures will aid in advancing the study of the evolution of animal sociality (Methion & Díaz López, 2020; Shizuka & Johnson, 2020), give new insights into cultural transmission and social learning (Allen, Weinrich, Hoppitt, & Rendell, 2013; Klump et al., 2021), contribute to wildlife and disease management (Rozins et al., 2018) and conservation efforts (Wiszniewski, Beheregaray, Allen, & Möller, 2010; Chiyo et al., 2011).

1.3 Parrot social and breeding systems

Detailed studies of parrot breeding behaviour and social structure in the wild are limited, perhaps as a result of the methodological and technical barriers involved in studying a taxon with high mobility, that is largely canopy dwelling, and is notoriously challenging to mark individually (e.g. Meyers, 1994). Despite parrots being considered largely monogamous (Arnold and Owens 1998), approximately 5% of species are reported to engage in cooperative breeding, and there are many species for which the mating system is unknown (Cockburn 2006), so the true number of cooperative parrot species may be underestimated. Monogamous parrots include the burrowing parrot, *Cyanoliseus patagonus* (Masello, Sramkova, Quillfeldt, Epplen, & Lubjuhn, 2002), and Bahama parrot, *Amazona leucocephala bahamensis* (Walker, 2016) amongst many others (Cockburn, 2006). Despite the number of parrot species reported to show an alternative mating system being relatively low, there is huge variation in these reported mating systems. For instance, joint nesting by potentially monogamous pairs has been reported in horned parakeet, *Eunymphicus cornutus* (Theuerkauf et al., 2009). There is female promiscuity combined with female-only offspring care in the greater vasa parrot, *Caracopsis vasa* (Ekstrom, Burke, Randrianaina, & Birkhead, 2007), and cooperative breeding with helpers, for example in the El Oro parakeet, *Pyrrhura orces* (Klauke et al., 2013), and the Santa Marta parakeet, *Pyrrhura viridicata* (Olaciregui, Oliveros-Salas, & Botero-Delgadillo, 2020). Cooperative polyandry with both sexes providing care has been detected in the Eclectus parrots, *Eclectus roratus* (Heinsohn, et al., 2007) and the New Caledonian parakeet, Cyanoramphus saisseti (Theuerkauf et al., 2009). Finally, the kakapo, *Strigops habroptilus*, makes use of leks in its breeding system (Merton, Morris, & Atkinson, 1984). There are many species with unknown or assumed mating systems amongst the Psittacidae, with some species having conflicting reports regarding the nature of their mating system (e.g. the kea, *Nestor notabilis*; Juniper & Parr 1998; Dussex & Robertson, 2018; and the monk parakeet, *Myiopsitta monachus*; Gonçalves da Silva, Eberhard, Wright, Avery, & Russello, 2010; Martínez, de Aranzamendi, Masello, & Bucher, 2013) with more detailed field studies required to uncover the diversity and frequency of parrot breeding and social systems.

1.4 Study species and study site

The monk parakeet, *Myiopsitta monachus* (Boddaert, 1783), is a sexually monomorphic, medium-sized parrot (weight 127-140 g, length 29 cm) native to temperate South America with a range from central Argentina to southern Brazil and central Bolivia (Forshaw, 1989). As a popular pet species, monk parakeets have been traded extensively within South America; wild-caught individuals constituted 97% of the trade in parrots within the continent between 2009-2010 (Bush, Baker, & Macdonald, 2014). They have also been exported in their thousands to meet the demands of the international pet trade (Russello, Avery, & Wright, 2008; Bush et al., 2014). Subsequently, deliberate or accidental release by pet owners combined with captivity breaches facilitated repeated invasions by monk parakeets across multiple continents (Forshaw, 1989; Russello et al., 2008; Van Bael & Pruett-Jones, 1996; Roll, Dayan, & Simberloff, 2008; Strubbe & Matthysen, 2009). Their widespread success as an invasive species has been attributed to a variety of traits, including behavioural and dietary flexibility (Bucher & Aramburú, 2014) and the thermoregulatory benefits provided by their large stick nests (Viana, Strubbe, & Zocche, 2016).

The monk parakeet is regarded as a crop pest in both its native and invasive range (Mott, 1973; Canavelli, 2011; Senar, Domènench, Arroyo, Torre, & Gordo, 2016), individuals occasionally build nests on power lines or in electricity substations causing power outages and safety concerns (Newman et al., 2008), and can carry diseases causing potential risks to humans (Menchetti & Mori, 2014; Raso, Ferreira, Timm, & de Fátima Tostes Abreu, 2014). In Europe, monk parakeets are among the invasive bird species that have the potential to cause the most acute impacts on the economy (Kumschick & Nentwig, 2010); indeed, extensive crop damage has already been detected in the agricultural zone bordering Barcelona city, Spain (Senar et al., 2016). However, despite the significant economic costs caused by populations of monk parakeets, little to no ecological costs have been detected on avifauna in the urban environment (Appelt et al., 2016). There is also some evidence of monk parakeets providing nest sites for other species in their native and invasive range and the species has therefore been described as an ecosystem engineer that provides a limiting resource to various secondary cavity nesters (Hernández-Brito et al., 2021). Various control methods are employed throughout both the native and invasive range to control or reduce the numbers of monk parakeets and limit the economic damage they cause (e.g. Newman et al., 2008). Such control methods include: the use of reproductive inhibitors (Yoder, Avery, Keacher, & Tillman, 2007; Avery, Yoder, & Tillman, 2008), lethal control, and nest destruction (Pruett-Jones, Newman, Newman, Avery, & Lindsay, 2007; Canavelli, 2011).

Monk parakeets are unique amongst parrots in their nest building behaviour. Interlaced sticks are used to construct large nest structures that can contain many individual nest chambers used by different pairs or groups year round for both roosting and breeding (Figure 3; Forshaw, 1989; Eberhard, 1998; Spreyer & Bucher, 1998). These nest structures vary in size; single nest structures have been reported to contain up to 100 pairs of parakeets (Naumberg, 1930), and have been recorded with 60 individual chambers (Burger & Gochfeld, 2005), but numbers typically reported are lower. For instance, in Catalonia the majority of nest structures contain only 1 or 2 chambers (Domènech, Carrillo, & Senar, 2003). Nests containing more than one chamber will hereafter be referred to as compound nests. Nests are frequently located within a larger group of nests occupying the same tree, and such clusters of nests in either the same or neighbouring trees are sometimes referred to as a colony (Bucher, Martin, Martella, & Navarro, 1991; Eberhard, 1998), however, there is a lack of clear delimitations between monk parakeet colonies. There have been no detailed investigations into the genetic relatedness of monk parakeets occupying the same compound nests or nesting trees, or into the demographic mechanisms driving any observed genetic structure, allowing opportunities for novel research into fine-scale kin structure in the monk parakeet and the demographic processes that drive it.

Reported dispersal distances for monk parakeets vary considerably, from a maximum of 2 km recorded in their native range in Argentina (Martín & Bucher, 1993) to over 100 km in their invasive range (North America) detected using genetic data (Gonçalves da Silva et al., 2010). Such long-range dispersal behaviour may facilitate the range expansion of monk parakeets and therefore their spread as an invasive species without further human assistance beyond introduction (Gonçalves da Silva et al., 2010). Although dispersing young have been recorded as moving singly, entire families have been recorded dispersing together following nest destruction (Martín & Bucher, 1993). Further investigations into natal and breeding dispersal behaviour in the monk parakeet would yield valuable insights into mechanisms driving population genetic structure, dispersal patterns in the urban environment, and could have implications for the management of monk parakeets as an invasive species.

Monk parakeets were thought to be sexually and socially monogamous (Navarro, Martella, & Bucher, 1995; Gonçalves da Silva et al., 2010), with evidence for sexual monogamy from both their native range in Argentina and their invasive range in North America (Gonçalves da Silva et al., 2010). However, recent investigations have suggested that monk parakeets in their native range in Argentina may be sexually polygamous, with extra-pair paternity detected in 40% of breeding chambers (Martínez et al., 2013), although this estimate was made without behavioural observations at the nest so breeding groups may have been overlooked. Furthermore, possible instances of intra-brood parasitism were also reported at the same location (Martínez et al., 2013). However, the evidence on mating patterns in this species is limited and further detailed investigations into the mating system would be fruitful.

Monk parakeets display several characteristics indicative of cooperative breeding, including limited dispersal and delayed breeding (Bucher, et al., 1991). In addition, there is some evidence of possible 'helpers' assisting breeding attempts (Bucher et al., 1991; Eberhard, 1998; Bucher, Martínez, & de Aranzamendi, 2016), with these 'helpers' observed aiding adults to feed young (Eberhard, 1998). However, very little research effort has been focussed on the exact nature of this 'helping' behaviour, its frequency, or the relatedness between 'helpers' and the young they help raise. Genetic evidence from a single breeding trio in South America points towards a high degree of relatedness in breeding groups; the male 'helper' was a full sibling of the breeding male (Bucher et al., 2016). However, current evidence for cooperative breeding in the monk parakeet is very limited and anecdotal, and genetic evidence and further field observations are needed to strengthen the conclusion that monk parakeets cooperate in breeding attempts and that additional group members direct aid towards kin. For individuals to be able to direct aid towards kin in the colonial, non-territorial social structure of monk parakeet populations, a mechanism of kin recognition may be needed for individuals to reliably discriminate kin from non-kin. A detailed investigation into patterns of breeding behaviour in monk parakeets would provide insights into the social and mating system of this unusual parrot species and add to our limited knowledge of parrot breeding systems in general.

Despite parrots being the subject of research on cognition and social evolution, relatively few studies have examined parrot social structure and associations in free-living individuals due to complexities of studying a mainly canopy-dwelling taxon. Some work has been done to examine social structure in the monk parakeet with evidence drawn from both unmarked wild flocks and captive groups providing some support for the idea that pairs constitute the main social unit, with frequent fission-fusion events between subgroups (Hobson, Avery, & Wright, 2014). However, there is scope for detailed investigations of monk parakeet social structure in a free-living population of marked individuals that would expand our understanding of social structure in this species but also in the Psittacidae more generally.

1.4.1 Study site and population

This study was conducted on the invasive, urban population of monk parakeets in Barcelona, Spain (41.39°N 2.17°E) on the north-east coast of the Iberian Peninsula. The core study and ringing area was Ciutadella Park (Figure 1), a large central park that covers approximately 30 ha and contains the zoological gardens of Barcelona and a large public access area of highly managed native and exotic vegetation. The first monk parakeet nests recorded in Barcelona were in Ciutadella Park in 1975 (Batllori & Nos, 1985), and since then this park has become an area of high monk parakeet nest density (J.C. Senar, personal communication; Figure 1). In Barcelona, monk parakeets exist at some of the highest densities found in Europe, and the population is expanding exponentially, doubling approximately every nine years (Domènech et al., 2003). Population estimates from 2015 approximated that 5000 monk parakeets were present in Barcelona (J.C. Senar, personal communication). The Barcelona population of monk parakeets is ideally suited for our study of social and genetic structure as the population has been consistently studied for almost 20 years and many individuals are uniquely identifiable through highly visible neck collars allowing identification at distances up to 40 m (Figure 2; Senar, Carrillo-Ortiz, & Arroyo, 2012). Each marked bird is also ringed with a Catalan Ornithological Institute aluminium leg ring. The distribution and expansion of the population has been tracked over many years with blood samples collected from individuals trapped in both the park and across the entire city, facilitating molecular genetic analyses and genetic sex-typing of individuals. Monk parakeets also regularly forage on the ground (Bucher et al., 1991), making them highly visible for observational work away from the nest.

During this study, we used a cherry picker to access nests, and nests under observation were labelled using laminated tags to facilitate observational work (Figure 3). Nests were visited multiple times across the breeding seasons and nestlings were ringed once reaching > 21 days of age (estimated from known monk parakeet growth rates; Carrillo-Ortiz, 2009). Blood samples (maximum 100 µl) are taken during ringing for genetic sex-typing and genetic analyses. At our study site individuals are also marked as adults when caught at either a baited food trap, using gas-propelled nets, or when incubating eggs or young.

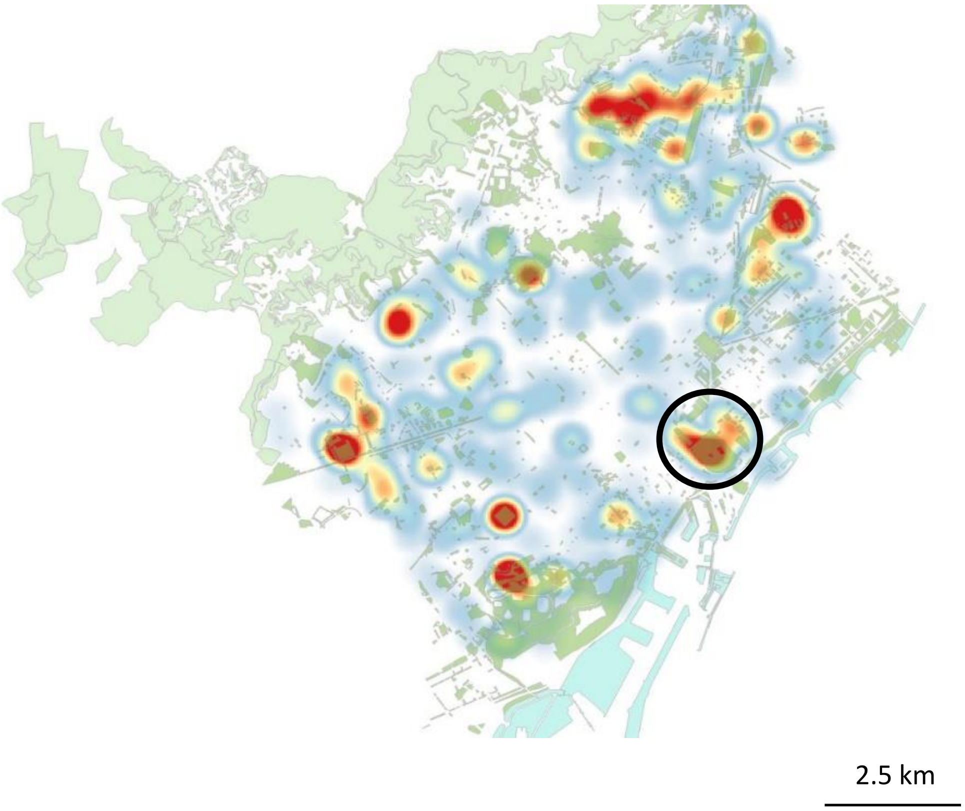

Figure 1. Heat map showing monk parakeet density and distribution in Barcelona, Spain (J. C. Senar, personal communication), focal study site; Ciutadella Park encircled.

Figure 2. Monk parakeets with unique medals worn on neck collars for identification of individuals, visible up to 40 m distance (methods from Senar et al. 2012).

Figure 3. Monk parakeet nests: a) a single chamber nest in a pine tree, b) a compound nest with two separate chambers in a pine tree, c) a single chamber nest in a palm tree and, d) two separate nests within the same pine tree. Laminated nest tags can be observed in a), b) and d).

1.5 Thesis aims and structure

The overarching aim of this thesis is to investigate the causes and consequences of the social and genetic structure of an unusual social parrot species, the monk parakeet, with a focus on the high density population living in Barcelona, Spain. In addition, I will examine the drivers of habitat selection in this worldwide invasive species and investigate the breeding system in detail.

In chapter 2, I detail the development of novel microsatellite loci for use in the monk parakeet; these microsatellite loci enabled the genetic analyses throughout my thesis. Using a genomic library, I describe the design of primer sets, evaluate these microsatellites in the monk parakeet, and optimise them in multiplex sets. I then examine the cross-species utility of these novel microsatellites by testing them in another invasive parrot species, the ring-neck parakeet, *Psittacula krameri*. Finally, I test sex-typing markers to identify sex-markers that will successfully sex individuals of both species.

In chapter 3, I investigate fine-scale genetic structure of the monk parakeet at a range of spatial scales, from birds sharing the same compound nests, to nests within the same nesting trees and to nests up to 400 m distant using spatial autocorrelation analyses. I then explore the demographic mechanisms driving the observed structure. Specifically, I relate genetic structure to patterns of natal and breeding dispersal, philopatry, site fidelity, and the formation of sibling coalitions using both field observations and molecular genetic techniques.

In chapter 4, I use observational field data to investigate the drivers of habitat selection in the monk parakeet, particularly during natal dispersal, with a focus on the potential influence of the natal environment in subsequent habitat choices. I also explore the potential for public information regarding conspecific breeding success to influence habitat selection and investigate ranging behaviour by recently fledged individuals to explore the relationship between ranging movements and dispersal behaviour.

In chapter 5, I characterise the social organisation and breeding system of the monk parakeet using detailed behavioural observations and molecular genetic techniques. I focus on three main objectives. First, I determine the frequency and composition of breeding groups and assess the route to group formation using social and genetic pedigrees. Second, I investigate the extent of cooperation and conflict in nest building and maintenance activities, including nest defence. Finally, I assess reproductive investment and productivity amongst pairs and breeding groups including an investigation into patterns of parentage in pairs and breeding groups.

In chapter 6, I explore the drivers of social associations away from the nest in the monk parakeet. Specifically, I test whether genetic relatedness among birds or inter-nest distance and hence familiarity drives social associations away from the nest. I also examine whether patterns are similar in same-sex and opposite-sex associations and whether social pairs and breeding groups are close social associates when away from the nest.

Finally, in chapter 7, I synthesise the results presented in this thesis and examine the findings in the wider context. I also suggest and discuss further avenues for research, building on the work presented here.

1.6 Statement of intellectual contributions

Research chapters (2-6) in this thesis are presented in the format of scientific manuscripts that have been greatly enhanced by collaboration and feedback of a number of colleagues. Professor Ben Hatchwell (BJH) acted as the primary supervisor for this project and the project was co-supervised by Dr Juan Carlos Senar (JCS) and Dr Daniel Franks (DWF). Contributions of all co-authors and collaborators are provided in detail below.

Chapter 2, Microsatellites: JCS supervised the field study and JCS and Alba Ortega-Segalerva collected the blood samples. Gavin J. Horsburgh and I conducted laboratory work at the NERC Biomolecular Analysis Facility, Sheffield, UK. Deborah A. Dawson and I analysed the data. MiSeq sequencing was performed by Dr Rebecca Thomas at the Sheffield Diagnostics Genetics Service at The Children's Hospital Sheffield supported by the Sheffield Children's NHS Trust, UK. Natalie dos Remedios provided training in the lab techniques. The work was funded by a UK Natural Environment Research Council (NERC) Biomolecular Analysis Facility (NBAF) grant (NBAF1078) to BJH, JCS and DWF. All authors contributed to revision of the manuscript for publication. This chapter is published as:

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Chapter 3, Population genetics: JCS and I conducted the fieldwork, I conducted laboratory work and DWF and I analysed the data. Thanks to Amy Leedale, Kathryn Maher and Jon Slate for advice regarding analyses and Alba Ortega-Segalerva, Danielle Mazzoni, Lluïsa Arroyo, Monica Navarro and volunteers for field assistance. All authors contributed to revision of the manuscript for publication. This chapter is published as:

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Chapter 4, Nest site selection: Alba Ortega-Segalerva, José G. Carrillo-Ortiz and I ringed birds and collected blood samples and conducted the fieldwork. I conducted laboratory work and analysed the data. Long-term data collected by JCS and colleagues at the Museu de Ciències Naturals de Barcelona. Chapter edited with comments from JCS, BJH and Francesc Uribe.

Chapter 5, Breeding system: I conducted the fieldwork with assistance from JCS, Alba Ortega-Segalerva and Danielle Mazzoni, I conducted laboratory work and analysed the data. Chapter edited with comments from BJH and JCS.

Chapter 6, Social associations: I conducted the fieldwork with assistance from JCS, Alba Ortega-Segalerva, Lluïsa Arroyo, Monica Navarro and volunteers, I conducted laboratory work and DWF and I analysed the data. Chapter edited with comments from DWF, BJH and JCS.

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2. Microsatellite characterisation and sex-typing in two invasive parakeet species, the monk parakeet *Myiopsitta monachus* and ring-necked parakeet *Psittacula krameri*

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2.1 Abstract

Invasive species can have wide-ranging negative impacts, and an understanding of the process and success of invasions can be vital to determine management strategies, mitigate impacts and predict range expansions of such species. Monk parakeets (*Myiopsitta monachus*) and ring-necked parakeets (*Psittacula krameri*) are both widespread invasive species, but there has been little research into the genetic and social structure of these two species despite the potential links with invasion success. The aim of this study was to isolate novel microsatellite loci from the monk parakeet and characterise them in both monk and ring-necked parakeets in order to facilitate future investigations into their behaviour and population ecology. Sex-typing markers were also tested in both species. Of the 20 microsatellite loci assessed in 24 unrelated monk parakeets, 16 successfully amplified and were polymorphic displaying between 2 and 14 alleles (mean = 8.06). Expected heterozygosity ranged from 0.43 to 0.93 and observed heterozygosity ranged from 0.23 to 0.96. Nine of the 20 loci also successfully amplified and were polymorphic in the ring-necked parakeet, displaying between 2 and 10 alleles. Suitable markers to sex both species and a Z-linked microsatellite locus were identified. A multiplex marker set was validated for monk parakeets. These novel microsatellite loci will facilitate fine and broad-scale population genetic analyses of these two widespread invasive species.

Keywords: Population genetics, microsatellite loci, sex markers, invasive species, Aves, Psittacidae.

2.2 Introduction

Invasive species are nonindigenous species that establish self-sustaining populations beyond their native range (Kolar & Lodge, 2001; Duncan, Blackburn, & Sol, 2003). The negative impacts of invasive species can be wide-ranging and include: extensive economic and environmental damage (Kumschick & Nentwig, 2010; Pimentel, 2011), threats to biodiversity (Bax, Williamson, Aguero, Gonzalez, & Geeves, 2003; Clavero & Garcia-Berthou., 2005) and damage to human health (Juliano & Philip Lounibos, 2005; Pyšek & Richardson, 2010). Two such invasive species are the monk parakeet (*Myiopsitta monachus*) and the ring-necked parakeet (*Psittacula krameri*).

As a popular pet species, tens of thousands of monk parakeets have been exported from their native South America to meet the demands of the international pet trade (Forshaw, 1989; Russello, Avery, & Wright, 2008; CITES: Trade Database). Subsequent breaches in captivity during transit or from holding areas, together with accidental or deliberate release by owners facilitated multiple invasion events across four additional continents (e.g. Forshaw, 1989; Russello et al., 2008). In Europe, monk parakeets are now among the invasive bird species with the potential to cause the most acute economic impacts (Kumschick & Nentwig, 2010). For example, substantial crop damage caused by foraging monk parakeets has been identified in the agricultural belt surrounding the city of Barcelona, Spain (Senar, Domènech, Arroyo, Torre, & Gordo, 2016); while in North America, their communal nests built on power lines and in electricity substations cause power outages and safety concerns (Newman et al., 2008).

Ring-necked parakeets, native to Asia and Africa (Forshaw, 1989), are the world's most widespread invasive parrot species, with populations reported in at least 35 different countries (e.g. Butler, 2003; Lever, 2005). Considered one of Europe's worst invasive species (Kumschick & Nentwig, 2010), ring-necked parakeets have wide-ranging negative impacts throughout their invasive range including outcompeting native cavity nesters for suitable nest-sites (e.g. nuthatches *Sitta europea*; Strubbe & Matthysen, 2009), killing native species through direct aggressive encounters (e.g. greater noctule bat *Nyctalus lasiopterus*; Hernández-Brito, Carrete, Ibáñez, Juste, & Tella, 2018), and causing severe economic damage (Kumschick & Nentwig, 2010).

Assessing the genetic structure of populations of invasive species can be key in understanding their origin and invasion history (Prentis et al., 2009), investigating dispersal patterns (la Rue, Ruetz, Stacey, & Thum, 2011), and determining eradication or management strategies (Abdelkrim, Pascal, Calmet, & Samadi, 2005). Microsatellites are molecular markers that are regularly used in such studies, and polymorphic markers have already been published for both monk parakeets (12 markers; Russello, Saranathan, Buhrman-Deever, Eberhard, & Caccone, 2007) and ring-necked parakeets (21 markers; Raisin, Dawson, Greenwood, Jones, & Groombridge, 2009). Here we present the characterisation of novel polymorphic monk parakeet microsatellite loci and their cross-species utility in the ring-necked parakeet. These new microsatellites, when used in combination with the microsatellite markers previously published for use in these species (Russello, et al., 2007; Raisin et al., 2009) will improve investigations into social and population genetic structure at a range of spatial scales, and help to examine the processes related to the invasion success of both species.

2.3 Materials and methods

2.3.1 Sampling and DNA extraction

Monk parakeet blood samples were collected in Barcelona, Spain (permit code: EPI 7/2015 (01529/1498/2015)) in May-July 2016 and 2017. Blood samples (maximum 100 µl) were taken from either the brachial or jugular vein of each individual, stored in 98% ethanol and kept at -20 °C before DNA extraction.

DNA was extracted overnight using an ammonium acetate extraction protocol (Nicholls et al., 2000; Richardson, Jury, Blaakmeer, Komdeur, & Burke, 2001). DNA quality was assessed by gel electrophoresis and its concentration quantified using a fluorimeter (FLUOstar Optima, BMG LABTECH Ltd., Aylesbury, UK). The library was constructed using genomic DNA extracted from a single female monk parakeet sampled in Barcelona, Spain. Genomic DNA was digested with *MboI* and enriched for dinucleotide (AG, AC) and tetranucleotide (CTAA, CTTT, GATA, GTAA) repeat motifs; magnetic beads were used in the enrichment hybridisation (modified from: Armour, Neumann, Gobert, & Jeffreys, 1994; Glenn & Schable, 2005). An Illumina paired-end library was generated using 1 µg of this repeat-enriched DNA. The NEBNext DNA Library Prep Kit for Illumina (New England Biolabs Inc.) protocol was followed and the DNA was sequenced using a MiSeq Benchtop Sequencer (Illumina Inc., San Diego, CA, USA). A total of 162 sequences that contained at least five tandem repeats were extracted from the data (EMBL-EBI accession numbers LR700312-LR700620). Twenty of these were selected and used to design primer sets.

2.3.2 Primer design and microsatellite evaluation

Primer pairs were designed using Primer3 v. 0.4.0 (Rozen & Skaletsky, 2000; Koressaar & Remm, 2007; Untergasser et al., 2012) in microsatellite flanking regions with a product size range from 100-270 bp. Further specifications for selecting primer pairs were: a melting temperature of 59-61 °C (optimum 60 °C, difference 0.5 °C), a length of 18 to 36 base pairs (20 bp optimum) the presence of a G/C clamp, a maximum poly-X of 3 tandemly repeating nucleotides (e.g. TTT), and all other parameters set to default. Forward primers were 5’-labelled with a fluorescent dye (HEX or 6-FAM). BLAST software (Altschul et al., 1997) was used to assess and select unique sequences for primer design.

DNA from 24 monk parakeets (12 male and 12 female) was amplified using polymerase chain reaction (PCR) to assess microsatellite variability. Monk parakeets are sexually monomorphic (Forshaw, 1989), therefore genetic sex-typing was used to determine the sex of individuals and to enable the identification of sex-linked microsatellite loci. Of nine bird sexing markers tested in monk parakeets, five were successful: P2-P8 (Griffiths, Double, Orr, & Dawson, 1998), P2D-P8 (Dawson et al., 2012), Z002B (Dawson, 2007), Z43B (Dawson, dos Remedios, & Horsburgh, 2016) and 2550F-2718 (Fridolfsson & Ellegren, 1999). Two of these sex markers were used in the present study (P2-P8 (Griffiths et al., 1998) and Z002B (Dawson, 2007)) to avoid any potential errors in sexing caused by misidentification of the Z and W alleles due to Z/W-polymorphism or the presence of heteroduplexes (Dawson et al., 2001; Robertson & Gemmell, 2006; Casey, Jones, Sandercock, & Wisely, 2009). PCR amplification was performed using a DNA Engine Tetrad ®Thermal Cycler (MJ Research, Bio-Rad, Herts, UK) in 2 µl reaction volumes containing 10-50 ng of air-dried DNA, 1 µl QIAGEN Multiplex PCR mix (containing PCR buffer, HotStarTaq DNA polymerase, 1.5 mM $MgCl_2$ and 0.2 µm dNTPs; QIAGEN Inc.) and 0.2 µM of each primer. Initial denaturation stage was carried out at 95 °C for 15 min, followed by a PCR amplification of 35 cycles (94 °C for 30 s, 58 °C for 90 s and 72 °C for 60 s) and a final extension for 30 min at 60 °C. Sex-typing markers P2-P8 and Z002B were amplified using annealing temperatures 50 °C and 56 °C respectively. 1 µl of PCR product was diluted to a ratio of 1:2500 - 1:5000 (product:H_2O) and these products were then separated on an ABI 3730 48-capillary DNA Analyser using formamide and GeneScan^{TM} -500 ROX size-standard (Applied Biosystems, Warrington, UK). Alleles were scored using GENEMAPPER v 5 software (Applied Biosystems, California, USA).

2.3.3 Data analysis

Allele numbers, polymorphic information content (PIC), estimated null allele frequencies, and observed (H_o) and expected heterozygosities (H_E) were calculated using CERVUS v3.0.7 (Kalinowski, Taper, & Marshall, 2007). Linkage disequilibrium and any departures from Hardy-Weinberg equilibrium were calculated using GENEPOP web version 4.2 (Rousset, 2008). In order to correct for multiple testing, a false discovery rate control (FDR) (Verhoeven, Simonsen, & McIntyre, 2005) was applied to p-values obtained for linkage disequilibrium. ML-RELATE was used to estimate maximum-likelihood coefficients of relatedness for each dyad (Kalinowski, Wagner, & Taper, 2006), confirming that the individuals used to characterise the microsatellite loci were unrelated ($r < 0.19$, mean ± SD = 0.02 ± 0.04).

2.3.4 Cross-species utility

Ring-necked parakeet blood samples were collected in November-March 2015-2017 in Barcelona, Spain (permit code: EPI 7/2015 (01529/1498/2015)). Blood samples (maximum 100 µl) were extracted from the jugular or brachial vein and stored at -20 °C in 98% ethanol. An ammonium acetate extraction protocol was used for DNA extraction (see above for details), PCR amplification was conducted on DNA extracted from 18 ring-necked parakeets (11 females and 7 males; sexed using P2-P8 (Griffiths et al., 1998) and Z002B (Dawson, 2007)), and microsatellite variability was then assessed as described for monk parakeets.

2.4 Results and discussion

2.4.1 Microsatellite characterisation

Of the 20 microsatellite loci tested, 17 successfully amplified and 16 were polymorphic in monk parakeets with allele numbers ranging from 2 to 14 with a mean of 8.06 alleles per locus (Table 2.1). H_O and H_E ranged from 0.23 - 0.96 and 0.43 - 0.93, respectively. PIC values ranged from 0.33 - 0.90 with 15 of the 16 microsatellite loci being highly informative (PIC > 0.50) and the other locus being reasonably informative (0.50 > PIC > 0.25; following (Botstein, White, Skolnick, & Davis, 1980)). One locus, MmonZ12, was heterozygous in some males (ZZ) yet homozygous in all 12 females (ZW) indicating it is sex-linked (Z-linked; Fisher's exact test, p = 0.004). All 15 other polymorphic loci amplified in both males and females, with no loci being homozygous in all females and all loci displaying heterozygotes in both males and females, and were therefore presumed to be located on the autosomes. For the Z-linked locus (MmonZ12), deviation from Hardy-Weinberg equilibrium was assessed in males only. Four loci (Mmon03, Mmon08, Mmon10 and Mmon13) exhibited significant deviations from Hardy-Weinberg equilibrium ($p < 0.05$), which may suggest the presence of null alleles. However, only one locus (Mmon08) possessed a high estimated null allele frequency (> 10%). Alternatively, deviations from Hardy-Weinberg equilibrium may result from population structure (Waples, 2015). Following FDR control, no significant linkage disequilibrium was found between loci. Multiplex Manager 1.2 (Holleley & Geerts, 2009) was used to generate a multiplex marker set from these 16 loci, optimised in three plexes; these multiplexes were then validated by genotyping the same 24 individual monk parakeets that had been genotyped in single-plex (Table 2.1).

Table 2.1 Characterisation of novel monk parakeet (*Myiopsitta monachus*) microsatellite loci (Psittacidae, Aves).

Locus, Accession	**Primer sequences (5' - 3'); forward (F); reverse (R)**	**Repeat motif**	**Multiplex**	**Observed allele size range (bp)**	**n**	**No. of alleles**	**H_O/H_E**	**Est. null allele freq.**	**PIC**
Mmon01 LR700312	F: [HEX] CCCACATGCTATGGTCCAG R: CTTCCAAGGATGAGGCAGAG	$(TTAG)_9$	3	177-201	23	7	0.70/0.72	0.001	0.67
Mmon02 LR700313	F: [6-FAM] AATCTCTAAAGAGGTCCACACTGC R: TGGATGTCTGAGGTGAACTCC	$(AC)_{16}$	1	141-173	24	10	0.96/0.89	- 0.05	0.85
Mmon03 LR700314	F: [6-FAM] TTTGCAGTGACCTTCATTCTG R: CTACAGCCAGCCTACTGTGC	$(TG)_{18}$	1	227-268	24	11	0.71/0.86**	0.09	0.83
Mmon04 LR700315	F: [HEX] ATCCTGCCTGTGAACTCTGG R: CCTCCCTCACCATTCCAAG	$(GT)_{20}$	1	220-243	24	10	0.75/0.85	0.06	0.81
Mmon05 LR700316	F: [HEX] TCCTGTCAAGGTGATGCTTG R: CTGTAGAAGATGGGAGGTTAGAGTG	$(CTAT)_{18}$	1	166-202	24	11	0.67/0.80	0.09	0.76
Mmon06 LR700317	F: [HEX] GGGAATTCAGTGGAAAGAGG R: CCCAAATCAGATTCTTGCTTC	$(CA)_{17}$	2	191-219	24	10	0.83/0.84	- 0.002	0.80
Mmon07 LR700318	F: [6-FAM] TGGCAGTATGAAACATACACACAG R: GGAAGCCACCAAGATTTCAG	$(ATCT)_{16}$	2	197-229	24	14	0.88/0.93	0.02	0.90
Mmon08 LR700319	F: [6-FAM] AAACCCAATGGCAGTGTTTC R: ACCATGGAGCTGAGGAACAG	$(TGGA)_7$	3	240-250	22	4	0.23/0.61**	0.44***	0.54
Mmon09 LR700320	F: [HEX] ATCCACAATCGTCAGATGGAG R: AAATGGGAAGTGAACCCAGAG	$(AC)_{13}$	3	136-148	24	6	0.71/0.70	- 0.01	0.64

Table 2.1 continued

Locus, Accession no.	Primer sequences (5' - 3'); forward (F); reverse (R)	Repeat motif	Multiplex	Observed allele size range (bp)	n	No. of alleles	H_O/H_E	Est. null allele freq.	PIC
Mmon10 LR700321	F: [6-FAM] TCAGTCAAGATGTTCCCTTGG R: GAGACAACAGCTCATCTTCCTCTAC	$(TG)_{14}$	3	90-101	24	7	0.75/0.81**	0.03	0.77
Mmon11 LR700322	F: [6-FAM] TGCAGTAATGATTTGATGCATTG R: ACAAGCACACCTCGCAAAC	$(TATC)_{11}$	3	153-173	24	6	0.71/0.72	0.01	0.67
MmonZ12 LR700323	F: [6-FAM] GCTTTCTCTGTGAAATCCATCC R: AACATCATCTTAAGAACCATCCAAG	$(ATCT)_6$	1	103-107	12M	2	0.58/0.43	- 0.17	0.33
			1	103-107	12F	2	0/0	NA	NA
Mmon13 LR700324	F: [6-FAM] CAGTATACCTATGGTTAAGGTTTCAGC R: CCTTGATTCAGATGGTAATTAGAGAAG	$(TCTA)_{14}$	3	122-144	24	6	0.88/0.79**	- 0.07	0.74
Mmon14 LR700325	F: [HEX] CTTTCTAACTCATTCCTAAGTGAGAGC R: GACTCTGTCTGACTCCTATTGCTG	$(GT)_{16}$	1	142-164	24	9	0.83/0.82	- 0.02	0.77
Mmon15 LR700326	F: [HEX] TTAAACAACAGTATTTGTGAGACCAAG R: TCCTTTCCAACCCTAACTATTCTG	$(AGAT)_{14}$	2	130-176	24	11	0.83/0.88	0.02	0.85
Mmon16 LR700327	F: [6-FAM] CAAACAGTCTTCCCTTTGTGG R: AAACACAGGCCCATCTGC	$(AC)_{12}$	2	141-167	24	5	0.67/0.65	- 0.03	0.57
Mmon17* LR700328	F: [HEX] AGGTCCTTTACAGCCCTAACTG R: GTTGAACTTCCCAGCTTTCC	$(TG)_{26}$	NA	254	22	1	NA	NA	NA

EMBL-EBI sequence accession numbers LR700312-LR700328, number of individuals results are based on (n), observed and expected heterozygosities (H_O and H_E respectively); ** Loci with significant departures from Hardy-Weinberg equilibrium; estimated null allele frequency (Est. null allele freq.), ***Mmon08 possessed high estimated null allele frequency (>10%), not applicable (NA); polymorphic information content (PIC). Mmon17* was monomorphic in monk parakeets and not included in the multiplex set.

2.4.2 Cross-species utility

Nine of the 20 microsatellite loci also amplified and were polymorphic in the ring-necked parakeet (Table 2.2). One of the nine loci polymorphic in ring-necked parakeets (Mmon17, Table 2.2) was monomorphic in monk parakeets and therefore was not included in the multiplex set for monk parakeets (Table 2.1). Allele numbers in ring-necked parakeets ranged from 2 - 10 (mean 5.22), H_O and H_E ranged from 0.12 - 0.89 and 0.11 - 0.89, respectively, and PIC values ranged from 0.11 - 0.85 (Table 2.2), with five loci being highly informative (PIC > 0.50), and one locus being reasonably informative (0.50 > PIC > 0.25; Botstein et al., 1980). MmonZ12 was also sex-linked in ring-necked parakeets (Fisher's exact test; $p < 0.001$), as in monk parakeets, but was more variable in ring-necked parakeets displaying a total of 10 different alleles in 18 individuals (Table 2.2). Z chromosome polymorphism was observed for both sex markers (P2-P8 and Z002B) in two out of 18 ring-necked parakeets (allele sizes: P2-P8 Z alleles 369 and 375 bp, W allele 403 bp; Z002B Z alleles 250 and 252 bp, W allele 234 bp) and was accounted for when assigning sex. Four loci (Mmon01, Mmon05, Mmon15 and MmonZ12) deviated significantly from Hardy-Weinberg equilibrium ($p < 0.05$) and two loci (Mmon03 and Mmon15) possessed a high estimated null allele frequency (>10%) in ring-necked parakeets. Linkage disequilibrium was significant between three pairs of alleles ($p < 0.05$; Mmon03 and Mmon04, Mmon04 and Mmon15, Mmon05 and Mmon15). However, this may be due to the presence of relatives in the sample of ring-necked parakeets used to characterise these microsatellite loci. ML-Relate (Kalinowski et al., 2006) indicated the presence of possible half-sibling (19/153) and full-sibling relationships (6/153) and one potential parent-offspring relationship among the 18 ring-necked parakeets sampled.

Table 2.2 Cross-species utility of monk parakeet (*Myiopsitta monachus*) microsatellite loci in the ring-necked parakeet (*Psittacula krameri*).

Locus	**n**	**No. of alleles**	**Observed allele size range (bp)**	**H_O/H_E**	**Est. null allele freq.**	**PIC**
Mmon01	17	6	165-193	0.71/0.78**	0.003	0.72
Mmon03	18	2	216-218	0.22/0.29	0.11***	0.24
Mmon04	18	3	204-207	0.39/0.48	0.07	0.41
Mmon05	18	10	127-176	0.83/0.89**	0.02	0.85
Mmon07	18	8	189-217	0.89/0.84	- 0.04	0.79
Mmon09	17	3	142-148	0.18/0.17	- 0.04	0.16
MmonZ12	7M	7*	201-245	1.00/0.88**	0	0.79
	11F	8*	205-245	0/0	NA	NA
Mmon15	17	6	138-155	0.35/0.80**	0.38***	0.74
Mmon17	17	2	218-226	0.12/0.11	- 0.02	0.11

Tested in 18 ring-necked parakeets; number of individuals results are based on (n), * a total of 10 different alleles were observed for MmonZ12, observed and expected heterozygosities (H_O and H_E respectively); ** Loci with significant departures from Hardy-Weinberg equilibrium; estimated null allele frequency (Est. null allele freq.), *** Mmon03 and Mmon15 possessed high null allele frequencies (>10%), not applicable (NA); polymorphic information content (PIC).

2.4.3 Limitations

DNA samples from monk parakeets and ring-necked parakeets used to characterise these microsatellite loci were taken from invasive populations for which there is no detailed knowledge of introduction events. Therefore, it is possible that these individuals are descendants from small founding populations which may have had limited genetic variation. On the other hand, both species have very extensive native ranges across South America (monk parakeet) and Africa and Asia (ring-necked parakeet) (Forshaw, 1989) and if founders were drawn from across these ranges, genetic variation of invasive populations may be greater than in local populations within their native range.

2.4.4 Conclusions

These novel microsatellite loci, optimised in three multiplexes, provide a powerful tool for analyses of both fine and broad-scale population genetic structure, as well as for analyses of parentage and dyadic relatedness. Combining these markers with those previously published for use in both monk parakeets (Russello et al., 2007) and ring-necked parakeets (Raisin et al., 2009) will facilitate detailed investigations into behavioural and population processes related to invasion success in these two widespread avian invaders. Such studies are likely to be particularly interesting in the case of monk parakeets given that they are highly social parrots, with unique compound nests made of sticks that may house many breeding pairs, often built in close proximity to other nests to form loose colonies (Forshaw, 1989; Bucher, Martin, Martella, & Navarro, 1990). Furthermore, examination of population genetic structure at a range of spatial scales may aid in the design of effective management strategies, help to understand the history of invasive populations and to predict future range expansions in these species.

2.4.5 Abbreviations

PCR: polymerase chain reaction; PIC: polymorphic information content; H_O: observed heterozygosity; H_E: expected heterozygosity; HWE: Hardy-Weinberg equilibrium; LD: linkage disequilibrium; EMBL-EBI: European Molecular Biology Laboratory – European Bioinformatics Institute; FDR: false discovery rate.

2.4.6 Compliance with ethical standards

Birds were handled and blood samples taken with special permission EPI 7/2015 (01529/1498/2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan regional ethical guidelines for the handling of birds. JCS received special authorization (001501-0402.2009) for the handling of animals in research from Servei de Protecció de la Fauna, Flora i Animal de Companyia, according to Decree 214/1997/30.07, Generalitat de Catalunya.

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3. Fine-scale genetic structure reflects limited and coordinated dispersal in the colonial monk parakeet, *Myiopsitta monachus*

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With running title: Kin structure of a social parrot population

3.1 Abstract

The genetic structure of animal populations has considerable behavioural, ecological and evolutionary implications and may arise from various demographic traits. Here, we use observational field data and molecular genetics to determine the genetic structure of an invasive population of monk parakeets, *Myiopsitta monachus*, at a range of spatial scales, and investigate the demographic processes that generate the observed structure. Monk parakeets construct large nests that can house several pairs occupying separate chambers; these nests are often aggregated within nesting trees. We determined patterns of relatedness within compound nests, within nesting trees and between trees. Spatial autocorrelation analyses of pairwise genetic relatedness revealed fine-scale genetic structure with relatives of both sexes spatially clustered within, but not beyond, nesting trees. In addition, males were more related to males sharing their compound nests than to other males occupying the same nesting tree. By contrast, males and females within compound nests were not significantly more closely related than elsewhere in the same tree, and we found no evidence for inbreeding. Adults showed high breeding site fidelity between years despite considerable disturbance of nest sites. Natal dispersal was female-biased, but dispersal distances were relatively short with some natal philopatry observed in both sexes. Sibling coalitions, typically of males, were observed amongst both philopatric and dispersing birds. Our results show significant clustering of kin within compound nests and nesting trees resulting from limited and coordinated natal dispersal, with subsequent breeding site fidelity. The resulting genetic structure has implications for social behaviour in this unusual parrot species.

Keywords: Population genetic structure, dispersal, philopatry, site fidelity, monk parakeet, *Myiopsitta monachus*

3.2 Introduction

Population genetic structure, that is the distribution and frequency of alleles and genotypes within and between populations, is a crucial demographic attribute that can have diverse behavioural, ecological and evolutionary implications. Genetic structure has consequences at a range of spatial scales, for instance, at fine scales, it can influence mate choice (Lee, Simeoni, Burke, & Hatchwell, 2010), cooperation (Leedale, Sharp, Simeoni, Robinson, & Hatchwell, 2018) and kin competition (West, Pen, & Griffin, 2002), whereas at broad spatial scales, it can result in local adaptation and even speciation (Papadopulos et al., 2014; Winker, McCracken, Gibson, & Peters, 2013). Limited dispersal due to geographical distance (isolation by distance), or physical barriers such as roads and rivers, can result in significant genetic structure (Garnier, Alibert, Audiot, Prieur, & Rasplus, 2004; Hayes & Sewlal, 2004; Riley et al., 2006; Wright 1943). However, physical barriers or large distances are not prerequisites for genetic differentiation; behavioural and life history traits can also generate genetic structure, for example, through natal philopatry (Leedale et al., 2018; MacColl, Piertney, Moss & Lambin, 2000; Solmsen, Johannesen & Schradin, 2011), site or group fidelity (Adams et al., 2006; Lee et al., 2010) and small effective population sizes (Beckerman, Sharp, & Hatchwell, 2011; Lehmann & Rousset, 2010).

Gene flow is ordinarily expected to be high in very mobile animals such as birds, such that genetic differentiation may be expected to be observed only at large spatial scales (Avise, 1996; Crochet, 2000). However, fine-scale genetic structure of adults following natal dispersal has been demonstrated across a variety of both cooperative and non-cooperative avian species, often driven by characteristic patterns of behaviour (e.g. Double, Peakall, Beck, & Cockburn, 2005; Lee, Jang, Dawson, Burke, & Hatchwell, 2009; Temple, Hoffman, & Amos, 2006; van Dijk, Covas, Doutrelant, Spottiswoode, & Hatchwell, 2015). For example, fine-scale kin structure in the colonial sociable weaver, *Philetairus socius*, is driven by natal philopatry and limited female-biased dispersal (van Dijk et al., 2015) whereas male-biased dispersal leads to significantly stronger genetic structure amongst females in the white-browed sparrow-weaver, *Plocepasser mahali*, (Harrison, York, & Young, 2014) and in some species of waterfowl (e.g. McKinnon, Gilchrist, & Scribner, 2006). Despite the potential for dispersal to disrupt kin-structured populations, there is also growing evidence from several species that dispersal in coalitions of relatives can maintain kinship ties and opportunities for kin-selected cooperation post-dispersal (e.g. Bradley, Doran-Sheehy, & Vigilant, 2007; Sharp, Simeoni, & Hatchwell, 2008; Williams & Rabenold, 2005). However, investigations of the occurrence of dispersal in kin coalitions are limited despite the implications for population genetic structure and cooperative behaviour (Sharp et al., 2008; Williams & Rabenold, 2005).

The spatial clustering of relatives has implications for the evolution of sociality, allowing cooperative behaviours to be directed towards kin resulting in kin-selected fitness benefits (Hamilton, 1964). For example, in vinous-throated parrotbills, *Paradoxornis webbianus*, clusters of male relatives in the breeding population result in increases in juvenile recruitment (Lee et al., 2009) and in the long-tailed tit, *Aegithalos caudatus*, genetic structuring in kin neighbourhoods provides opportunities for indirect fitness benefits through helping at relatives' nests (Leedale et al., 2018). However, such spatial aggregations of relatives may also increase kin competition (Moore, Loggenberg, & Greeff, 2006; Platt & Bever, 2009; West et al., 2002) and the risk of inbreeding (Brouwer, van de Pol, Atema & Cockburn, 2011; Lukas & Clutton-Brock, 2011; Nelson-Flower, Hockey, O'Ryan, & Ridley, 2012).

A limited number of studies have combined investigations of fine-scale genetic structure among post-dispersal adults with a detailed examination of the potential mechanisms driving the observed structure. Therefore, the processes generating structure and its behavioural, ecological and evolutionary implications require further investigation. This is particularly true of dispersal, which is inherently challenging to study (Koenig, Van Vuren, & Hooge, 1996). Investigations combining behavioural field data and molecular genetics can provide detailed insights into the genetic structure of populations and reveal the demographic mechanisms driving it. Here we investigate fine-scale population genetic structure in a worldwide invasive parrot species, the monk parakeet (*Myiopsitta monachus*), and examine key demographic characteristics behind the observed structure. The monk parakeet is a sexually monomorphic species native to South America (Forshaw, 1989) that thrives in the urban environment and has become established throughout the world through escapes from the pet trade (Bush, Baker, & Macdonald, 2014; Lever, 2005; Russello, Avery, & Wright, 2008).

Monk parakeets are unique amongst parrots in their nest building behaviour, using interlaced sticks to construct large nest structures that are used year round for roosting and breeding (Eberhard, 1998; Forshaw, 1989; Spreyer & Bucher, 1998). Nest structures vary in size from those containing a single nest chamber to compound nests containing up to 100 pairs, each occupying a separate nest chamber (Naumberg, 1930). However, numbers are typically lower; for instance, in Catalonia, the majority of nests structures contained only 1 or 2 chambers in 2001, although nests with up to 36 chambers were detected (Domènech, Carrillo & Senar, 2003). Nests containing more than one chamber are referred to hereafter as compound nests. Nest chambers are occupied most commonly by pairs of birds, however the occurrence of trios occupying nest chambers has been reported (Bucher, Martin, Martella, & Navarro, 1990; Eberhard, 1998). Nests are often spatially clustered in groups occupying the same or neighbouring trees; these aggregations have been referred to as colonies (Bucher et al., 1990; Eberhard, 1998), however, due to a lack of clear delimitations between monk parakeet colonies we conduct analyses at the level of compound nests, within nesting trees, and between trees. There have been no previous investigations into the genetic structure of monk parakeets at these fine spatial scales.

Using a combination of field observations and molecular genetics we first assessed whether there was significant inbreeding or outbreeding at our study site. Second, we investigated the fine-scale spatial genetic structure of adult monk parakeets to determine whether relatives were spatially clustered within nesting trees and whether any genetic structure extended beyond the nesting tree. We then investigated whether relatives were clustered in compound nests within nesting trees. Finally, we examined the demographic mechanisms generating kin structure in the monk parakeet including: adult breeding site fidelity, natal dispersal and philopatry, and the coordinated dispersal of sibling coalitions.

3.3 Materials and methods

3.3.1 Study site

This study was conducted in Barcelona, Spain (41.39°N 2.17°E), on the north-east coast of the Iberian Peninsula. We conducted surveys across the city of Barcelona with the majority of fieldwork conducted in Ciutadella Park, a large (c. 30ha) central park in the city that contains the city's zoological gardens and a large public access area of highly managed native and exotic vegetation. Ciutadella Park is the site of the first record of monk parakeet nests in Barcelona (Batllori & Nos, 1985) and now contains a high density of monk parakeet nests.

3.3.2 Sample collection

For ringing, monk parakeets were either caught in a baited trap controlled remotely, using gas propelled nets, or in nest chambers either prior to fledging or as incubating adults. A cherry picker was used for nest access in these cases. No birds abandoned their nests as a result of disturbance caused by nest checks or by ringing. Each bird was ringed with an aluminium leg ring and also marked with a unique neck collar for visual identification in the field at distances of up to 30-40 m

(Senar, Carrillo-Ortiz, & Arroyo, 2012) allowing behavioural observations and the identification of nesting locations. During ringing, blood samples (maximum 100 µl) were collected for genetic analyses and sex determination.

3.3.3 Compliance with ethical standards

Birds were handled and blood samples taken with special permission EPI 7/2015 (01529/1498/2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan regional ethical guidelines for the handling of birds. JCS received special authorization (001501-0402.2009) for the handling of animals in research from Servei de Protecció de la Fauna, Flora i Animal de Companyia, according to Decree 214/1997/30.07.

3.3.4 Nest observations

To determine nesting locations of adult monk parakeets during the breeding season, we conducted detailed behavioural observations between April and July 2018 at 10 large, mature pine trees in Ciutadella Park that contained monk parakeet nests. During the breeding season, marked individuals were never observed to enter a chamber that they did not use as their roosting or breeding chamber (F.S.E.D.P. personal observation), so we are confident that individuals recorded entering or leaving chambers were the occupants of that chamber. We conducted 263 hours of behavioural observations at a total of 72 nests that contained 149 individual nest chambers. These nests were occupied by 113 marked individuals and at least 64 unmarked individuals during the period of observation. Blood samples were available for genetic analysis from 112 of the marked birds. GPS coordinates of each nesting tree were recorded; all monk parakeets with nests in the same tree were assigned the same spatial coordinates. Distances between nesting trees were calculated from GPS locations and used to inform distance bands in the spatial analysis of genetic relatedness (see *Spatial genetic structure*).

3.3.5 DNA extraction and genotyping

For details of blood sample storage and DNA extraction see Dawson Pell et al., (2020). We used 26 microsatellite markers optimised in 6 multiplexes (for details see Supplementary Material Table S3.1). These markers were: Mmon01, Mmon02, Mmon03, Mmon04, Mmon05, Mmon06, Mmon07, Mmon09, Mmon10, Mmon11, Mmon13, Mmon14, Mmon15, Mmon16 (Dawson Pell et al., 2020), MmGT012, MmGT090, MmGT054, MmGT060, MmGT046, MmGT105, MmGT030, MmGT071, MmGT057 (Russello, Saranathan, Buhrman-Deever, Eberhard, & Caccone, 2007), TG03-002 and TG05-046 (Dawson et al., 2010), CAM-20 (Dawson et al., 2013). PCR and allele scoring protocols were the same as those followed in Dawson Pell et al., (2020). Alleles were scored blind to bird identity. Allele scoring error was examined for these markers for a concurrent study of monk parakeet behaviour; based on repeat genotyping of 50 individuals, scoring error was estimated at 3.1% (F.S.E.D.P. unpublished data). Monk parakeets are sexually monomorphic in the field (Forshaw, 1989), so individuals were sex-typed using a sexing marker, Z002B (Dawson, 2007).

3.3.6 Assessing marker quality

Estimated null allele frequencies were calculated using Cervus v3.0.7 (Kalinowski, Taper, & Marshall, 2007). One locus (MmGT054) possessed high estimated null allele frequencies (> 10%) and was excluded from further analyses. Both linkage disequilibrium and departures from Hardy-Weinberg equilibrium were assessed using GENEPOP web version 4.2, using 100 batches of 1000 iterations (Rousset, 2008). A false discovery rate control (FDR; Verhoeven, Simonsen, & McIntyre, 2005) was applied to p-values obtained for both tests to correct for multiple testing. Following FDR control, departures from Hardy-Weinberg equilibrium were detected for four loci (Mmon05, Mmon06, MmGT090, MmGT012) so these loci were not included in any further analyses. The presence of relatives was assessed using ML-Relate (Kalinowski, Wagner, & Taper, 2006) and close relatives were removed before analyses of linkage disequilibrium, resulting in 45 individuals being used in linkage assessment. No significant linkage disequilibrium was found between loci. Heterozygotes were observed for both males and females at each of the remaining 21 loci, indicating these markers are located on the autosomes in monk parakeets. We therefore used 21 polymorphic microsatellite loci in all further analyses.

3.3.7 Spatial genetic structure

To investigate the overall population genetic structure of adult monk parakeets and assess whether mating occurs randomly within our study population we used two measures. First, we used R_{IS}, a microsatellite allele size-based genetic differentiation estimate (Rousset, 1996; Slatkin, 1995); secondly, we used F_{IS}, Weir and Cockerham's (1984) inbreeding coefficient. Both measures were calculated in SPAGeDI v. 1.5 (Hardy & Vekemans, 2002); alleles were permuted among individuals 20,000 times and multilocus estimates were jackknifed over loci in order to calculate estimates of differentiation and approximate standard error of genetic relatedness.

To investigate fine-scale genetic structure in our population of monk parakeets, we conducted spatial autocorrelation analyses of pairwise genetic relatedness (r_{QG}; Queller & Goodnight, 1989) between individuals as a function of the geographic distance between their nesting tree locations. Some nests are built in trees in close proximity to each other, but in the absence of clear and objective delimitation between monk parakeet 'colonies', we use nesting tree as the level of analysis. We used a Cartesian coordinate system (UTM) to determine geographic distances between nesting trees in these analyses. Spatial analyses were conducted in SPAGeDI v. 1.5 (Hardy & Vekemans, 2002) over six distance bands: 0 m for analyses of birds within the same nesting tree, from >0-25 m, from 25-100 m, then increments of 100 m to a maximum of 400 m distance between nesting trees. Observed distances between nesting trees ranged from 5 m to 382 m and the chosen distance bands generated sufficiently large sample sizes to ensure meaningful analyses whilst making sure statistics computed for each distance interval were not based on small fractions of the available individuals (see Figure 3.1 for the number of pairwise comparisons per distance band). We conducted these analyses separately for: (a) all individuals, (b) males, (c) females and (d) between males and females. Mean observed r_{QG} values calculated for each distance band in our population were compared to distributions of r_{QG} values generated using 20,000 random permutations of individual nest locations and all tests were two-tailed. For all analyses, we considered the observed r_{QG} to be statistically significant if it fell outside of the 95% confidence interval of the random distribution generated by data permutations.

3.3.8 Relatedness within compound nests

To investigate relatedness within compound nests, we first determined the number of compound nests in our study site and identified their occupants; we excluded any nests with more than one chamber where all the chambers were used by the same individuals, as these individuals could be considered one pair/group sharing multiple chambers, rather than separate pairs/groups with individual nest chambers. To examine whether males sharing a compound nest were more closely related to each other than to other males nesting in the same tree, we constructed a multi-membership GLMM with the MCMCglmm package (Hadfield, 2010) using default priors. We included nesting tree as a random intercept to account for repeated measures, and the identities of the individuals within relatedness dyads were included as multi-level random effects because relatedness is an undirected relationship. MCMCglmm automatically adds a random intercept at the level of the dyad. We ran the default number of MCMC iterations and used the default burnin, with a thinning interval of 10. We then randomly permuted relatedness between dyads within nesting trees and refitted the model 999 times, and then compared the effect size from the original model to those from models fitted to the permutations to calculate p-values for a one-tailed test. Statistical tests were carried out in R 3.5.0 (R Core Team 2018). For these analyses, the genetic relatedness between dyads was estimated using Queller and Goodnight's (1989) r_{QG} coefficient of relatedness in SPAGeDI v. 1.5 (Hardy & Vekemans, 2002). Datasets included relatedness values for males that share compound nests and relatedness values between the males that occupied compound nests and the other males occupying different nests in the same nesting tree. We repeated the same analysis on two more conservative datasets. First, we excluded from the dataset the relatedness values of male dyads that shared the same nest chamber. This analysis removed within chamber comparisons that could bias the results if close kin share breeding chambers. Secondly, we randomly selected a single bird from multi-male chambers and included only the relatedness values between this bird and other males sharing its compound nest in the dataset because again closely related males sharing a nest chamber could bias the relatedness values within a compound nest. This analysis also excluded relatedness values for males sharing the same nest chamber, as described above.

To examine whether males were more related to females sharing their compound nest than to other females in the same nesting tree, we repeated the process described for males. For this analysis we excluded relatedness values of known pairs. We corrected for multiple comparisons using the Bonferroni correction in each of the above analyses, resulting in $\alpha = 0.0125$. Relatively few females in compound nests were marked, therefore we were unable to conduct equivalent analyses comparing female relatedness in compound nests and nesting trees.

Ideally we would also have examined whether compound nest associations between individuals persist over time in order to examine long-term cooperative associations between individuals. However, all nests were removed in 2018 so we were unable to examine such associations. Nest removal is used as an invasive species management strategy for monk parakeets in Barcelona as it is elsewhere in both the native and invasive range (Pruett-Jones, Newman, Newman, Avery, & Lindsay, 2007).

3.3.9 Breeding site fidelity

We examined breeding site fidelity of adult birds by comparing occupation of nesting trees during the breeding season (March-September; Senar et al., 2019) across years. Individually marked birds were located in the 10 pine trees in Ciutadella Park during censuses undertaken in 2017. In 2018 and 2019 marked birds were then located in the 10 pine trees by detailed behavioural observations totalling 387 hours. Beyond the focal 10 trees, marked birds were located during surveys of nests in

Ciutadella Park or in surveys of monk parakeet nest sites across Barcelona up to 6 km from Ciutadella Park. Over 380 hours were spent surveying colonies across Barcelona for marked individuals in 2018 and 2019. Birds were recorded as the nest occupants only if they were observed either in a nest chamber or bringing nest material to a nest; birds that were only observed perched in a tree that contained a nest were not recorded as nest occupants. We determined the number of marked birds that bred in the same or different trees between years and across all three years to assess site fidelity. We used previously calculated survival estimates for monk parakeets in our study location to approximate survival between years (Conroy & Senar, 2009). We used the GPS coordinates of nesting trees to calculate breeding dispersal distances for birds that were detected in a different nesting location between years in R using the distGeo function from the geosphere package (Hijmans, Williams, & Vennes, 2019). We tested for sex differences in breeding dispersal distances using a Wilcoxon rank sum test.

In addition, we used data from a concurrent study into social associations of monk parakeets (F.S.E.D.P. unpublished data) to search for marked target birds not identified at a nest to corroborate our calculations of the number of putative survivors. These data were collected opportunistically on encountering marked birds away from nests (F.S.E.D.P. unpublished data). We examined social groups recorded over the breeding seasons (March-Sept) in 2018 and 2019 for sightings of target birds not located at nests, enabling calculation of the total number of surviving birds seen either at nests or elsewhere.

3.3.10 Natal philopatry and dispersal

To investigate natal dispersal in the monk parakeet, we ringed nestlings during the breeding seasons (March-August) in 2017 and 2018, using a cherry picker to access nests. In 2017, we ringed nestlings in Ciutadella Park, Passeig de Lluís Companys, and Plaça de Tetuan; in 2018 nests were accessed only in Ciutadella Park and Passeig de Lluís Companys. Nestlings more than c.21 days old were removed briefly from nest chambers and marked with aluminium leg rings and unique medals attached to neck collars, as detailed in *Sample collection*. Blood samples were also taken for sex determination and genetic analyses as above.

We followed classical definitions of natal dispersal (e.g. Greenwood & Harvey, 1982) and determined the distance between natal nests and the nests occupied during each individual's first breeding season post-fledging. In a previous investigation into the breeding activity of one-year-old birds at our study site, 55% were engaged in a breeding attempt as a member of a pair, and a further 18% were part of a trio, although it was not confirmed whether one-year olds in trios were parents to any offspring (Senar et al., 2019). Thus, one-year-old monk parakeets are sexually mature, although not all individuals engage in breeding attempts in their first year post-fledging. We recorded the GPS coordinates of natal trees and the nesting trees of marked birds located during the breeding season in their first year post-fledging (2018 or 2019) in the surveys detailed in *Breeding site fidelity*. Natal dispersal distances were calculated for each bird in R with the distGeo function (Hijmans et al., 2019) using the GPS coordinates of their natal and first-year nesting trees. Finally, we tested for a sex difference in natal dispersal distances using a Wilcoxon rank sum test.

3.4 Results

3.4.1 Genotypes and estimation of inbreeding

Marked adults (total genotyped = 112; 46 females, 66 males; age range 1-12+ years) recorded nesting in the 10 focal pine trees in 2018 were genotyped at 21 microsatellite loci (multilocus averages across all individuals: individual inbreeding coefficient F_I = -0.006, mean allele number per locus = 7.33, allelic richness = 6.60, effective alleles = 4.06 (Nielsen, Tarpy, & Reeve, 2003), observed heterozygosity = 0.66 and gene diversity corrected for sample size = 0.65). A total of 154 unique alleles were detected in our population (range of allele numbers per locus = 2–17). For the distribution of allele number by locus, observed and expected heterozygosity and observed allele size ranges see Supplementary Material Table S3.2. We detected no significant outbreeding or inbreeding in our study population; the average genetic variation among individuals did not differ significantly from random (based on 20,000 permutations, microsatellite-specific genetic differentiation estimate $R_{IS} = -0.003 \pm 0.027$ SE, $p = 0.93$; population inbreeding coefficient $F_{IS} = -0.007 \pm 0.015$ SE, $p = 0.56$).

3.4.2 Spatial genetic structure

Spatial autocorrelation analyses revealed significant fine-scale genetic structure in our study population (Figure 3.1). Mean ± SE relatedness within nesting trees was 0.027 ± 0.01 for all individuals, 0.028 ± 0.01 for males, 0.013 ± 0.01 for females and 0.021 ± 0.01 between males and females, with SE calculated by jackknifing over loci. In all cases, pairwise relatedness within nesting trees was higher than expected by chance (all $p < 0.02$; Figure 3.1; based on 20,000 data permutations), indicating that relatives are clustered in nesting trees. Significant genetic structuring was not found beyond the level of the nesting tree, even between trees <25 m away, until the 300-400 m distance band that indicated individuals separated by this distance were less related to each other than expected by chance for all individuals ($p = 0.011$) and between the sexes ($p = 0.004$); no significant structure was found at this distance for either males ($p = 0.19$) or females ($p = 0.39$).

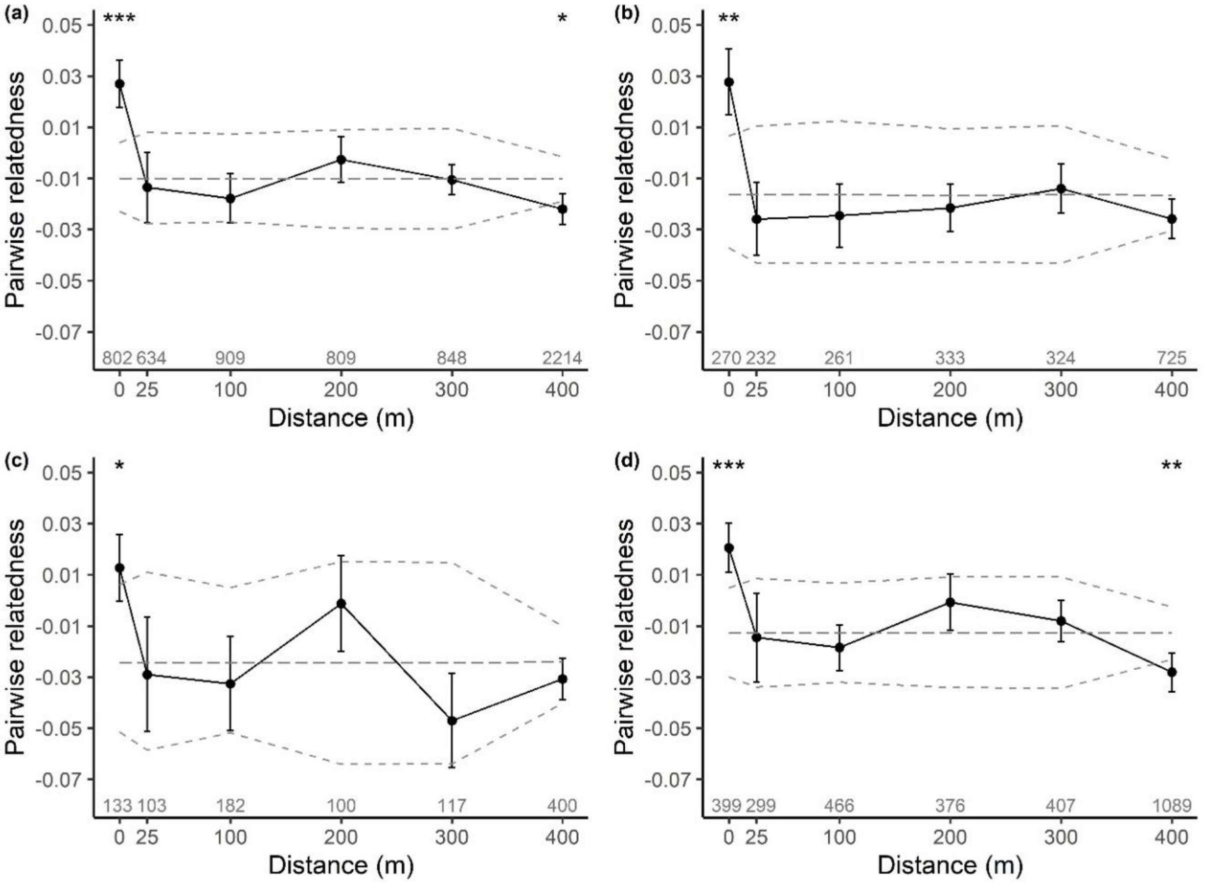

Figure 3.1. Mean pairwise relatedness ± SE within nesting trees (0 m distance) and over five further distance bands of inter-tree distances: (a) among all individuals, (b) among males, (c) among females and (d) between males and females. Error bars generated by jackknifing over loci to approximate SE. Null mean pairwise relatedness and 95% CI generated through 20,000 data permutations indicated by dashed lines. Number of pairwise comparisons indicated above the x-axis for each distance band. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

3.4.3 Relatedness within compound nests

Thirteen (18.1%) of the 72 observed nests housed more than one pair of birds using separate chambers. The relatively small overall number of compound nests in our population may be due to management practises at our study location that regularly involve nest removal. For analysis of relatedness of males within compound nests, we excluded any compound nests with just one marked male, leaving 24 suitable males from nine compound nests in five separate nesting trees to include in analyses. Seven of these compound nests housed two separate groups of monk parakeets and two nests had three separate groups occupying different nest chambers. Relatedness between males sharing a compound nest was on average 0.199 higher than relatedness of those males to the other males in the same nesting tree when including relatedness values for all male dyads in a compound nest (posterior mean = 0.199, 95% Credible Intervals = 0.127-0.276, $p < 0.001$; Figure 3.2a). More conservative analyses gave qualitatively similar results: when within chamber comparisons were excluded from the dataset (posterior mean = 0.183, 95% Credible Intervals = 0.100-0.271, $p < 0.001$; Figure 3.2b), and when a single male from multi-male chambers was randomly selected for comparison with other males in the same compound nest combined with within-chamber exclusion (posterior mean = 0.183, 95% Credible Intervals = 0.109-0.269, $p < 0.001$; Figure 3.2c).

We also compared the relatedness between males and the females that shared their compound nest to the relatedness between those males and all other females in the same nesting tree for 14 males from eight compound nests located in five different nesting trees. These compound nests comprised six nests occupied by two separate groups of monk parakeets and two nests containing three groups occupying separate nest chambers. In contrast to our findings for male-male relatedness, there was no significant difference between the relatedness of males to females that share a compound nest compared to the females occupying the rest of the same nesting tree with the Credible Intervals overlapping zero (posterior mean = 0.079, 95% Credible Intervals = -0.038-0.200, $p = 0.114$; Figure 3.2d).

The clustering of male relatives within compound nests could potentially drive the significant spatial genetic structure observed for males and for all birds within nesting trees, as described in the previous section. Therefore, we conducted additional spatial autocorrelation analyses for males and for all birds using the same distance bands as described previously, but randomly selected one male only from each compound nest to be included in analyses (for additional details see Supplementary Material S3). Our results were qualitatively similar to those we obtained when all males in compound nests were included in the analyses (Supplementary Material S3; Figure S3.1), demonstrating that the significant spatial genetic structure of males and of all birds within nesting trees was not simply a function of kin being clustered in compound nests, but must also result from kin being clustered within trees.

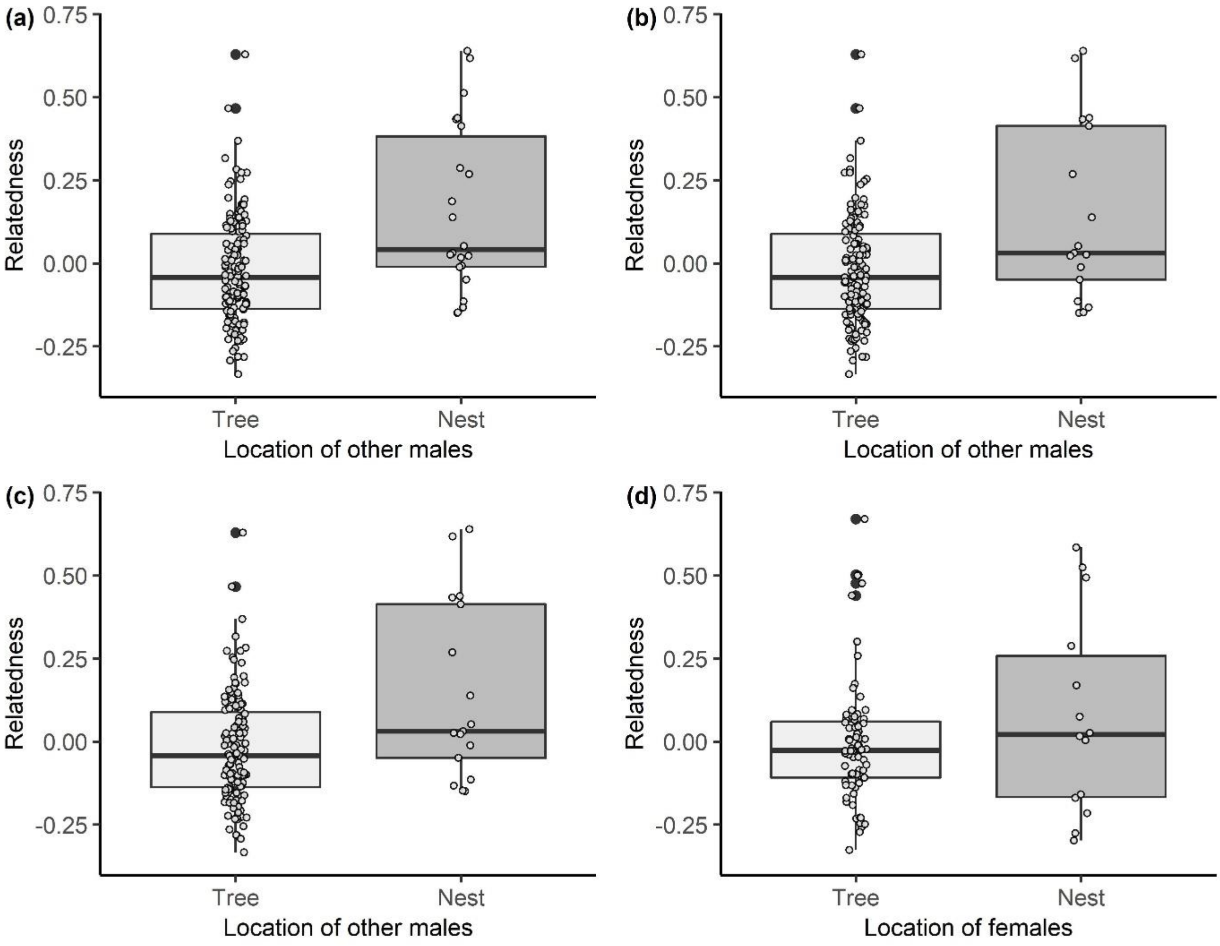

Figure 3.2. Dyadic genetic relatedness of individuals from compound nests to birds sharing the same compound nest and to birds occupying other nests in the same nesting tree for: (a) males compared to all other males sharing their compound nests and to males occupying other nests in the same nesting tree ($p < 0.001$); (b) males compared to other males sharing the same compound nest, excluding within chamber comparisons, and to males occupying other nests in the same nesting tree ($p < 0.001$); (c) males compared to other males sharing the same compound nest with random selection of males from multi-male chambers and excluding within chamber comparisons, and to males occupying other nests in the same nesting tree ($p < 0.001$); and (d) males compared to females in the same compound nest, excluding mate comparisons, and to other females occupying other nests in the same nesting tree ($p = 0.114$). Boxplots indicate: the interquartile range (box upper and lower limits), median relatedness values (thick lines within boxes), minimum and maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

3.4.4 Breeding site fidelity

In the 2017 breeding season, we located 72 marked adults (23 female, 38 male, 11 unknown sex) in the 10 focal pine trees; 46 (64%; 16 female, 30 male) bred in the same tree in 2018 and 25 (54%; 9 female, 16 male) of these bred in the same location for a third consecutive year in 2019. In 2018, a total of 113 marked birds (46 female, 66 male, 1 unknown sex, including the 46 still present from 2017) were located in the 10 focal pine trees and 51 (45%; 21 female, 30 male) remained in the same nesting tree in 2019. Thus, estimated annual site-fidelity ranged from 45-64%, although this disregards the fact that some of the birds not located again were likely to have died between breeding seasons.

The estimated annual survival rate for monk parakeets in our study site is 0.82 (Conroy & Senar, 2009). Therefore, of the 72 birds alive in 2017 we would expect 59 to have survived to 2018; 46 (78%) of these 59 putative survivors were observed to be faithful to their breeding site. Of the 112 birds alive in 2018 (one bird found dead in their nest during the 2018 breeding season was excluded from the total), 92 were likely to have survived to 2019, but just 51 (55%) of these putative survivors remained in the same nesting tree. However, it is important to note that in July 2018, all nests in the 10 focal nesting trees were removed by park authorities due to the risk they posed to the public. The apparently lower site fidelity in 2018-2019 relative to 2017-2018 may have been a consequence of this nest destruction.

In addition, we recorded 23 breeding dispersal events that involved adult birds moving between our 10 focal trees. During more extensive surveys in the rest of Ciutadella Park and across Barcelona to detect breeding dispersers we located the nests of 92 marked adult birds, only two of which had dispersed from one of the focal trees. In total therefore, we recorded 25 breeding dispersal events by 24 birds (11 female, 13 male), 21 (84%) of which occurred following nest destruction in 2018. The median breeding dispersal distance for all dispersers was 37 m (range = 5-464 m, mean = 87 m ± 103

SD, N = 25 dispersal events), and there was no significant difference between the breeding dispersal distances of males and females (Z = -0.30, p = 0.76, N = 25; Figure 3.3).

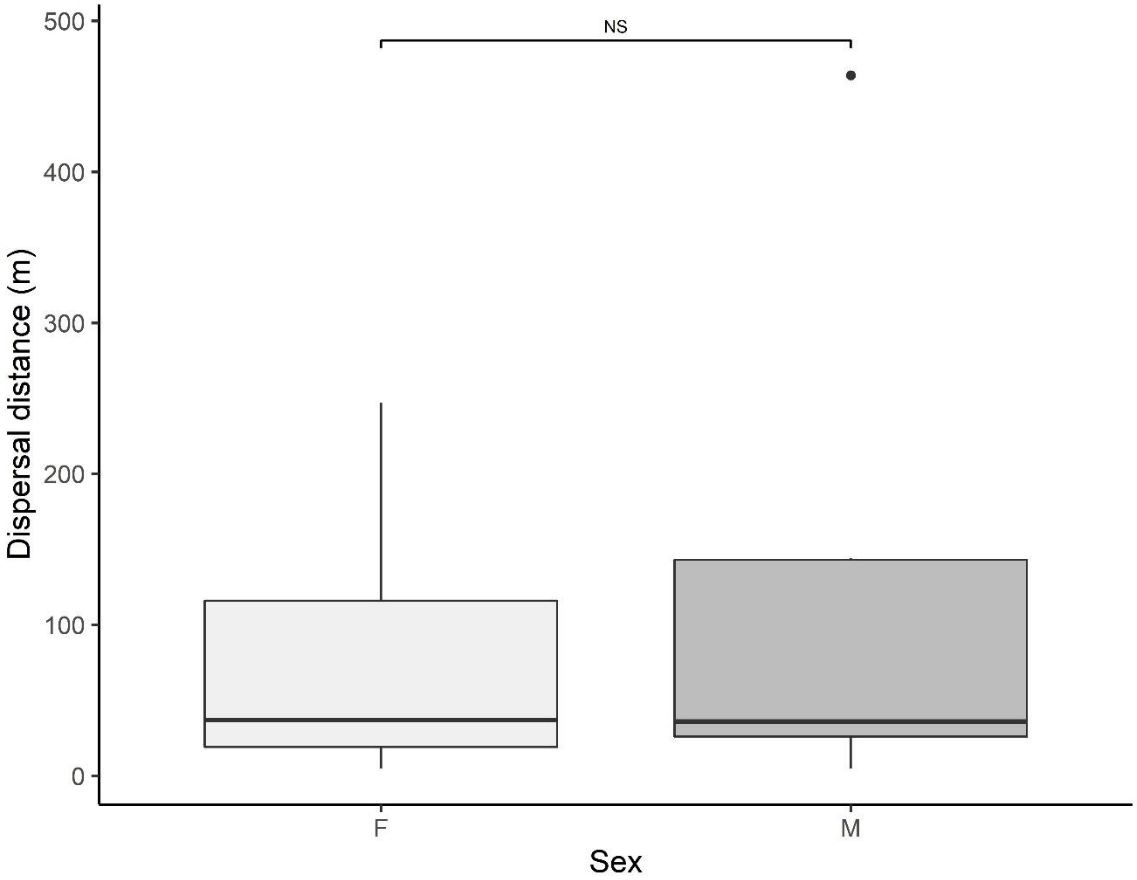

Figure 3.3. Breeding dispersal distances for monk parakeet; females (F; N = 11 dispersal events) and males (M; N = 14 dispersal events). Boxplots indicate: the interquartile range (box upper and lower limits), median dispersal distances (thick lines within boxes), minimum and maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

Using data collected for a concurrent study of monk parakeet social associations (F.S.E.D.P. unpublished data), we identified 12 birds in 2018 and 6 birds in 2019 that had survived from the previous breeding season but whose nest locations were unknown. Taken together, we therefore sighted 62 birds (86%) in 2018 out of the 72 that nested in the 10 focal pine trees in 2017, and a total of 78 birds (70%) in 2019 out of the 112 that nested in the 10 trees in 2018. Therefore, the total numbers of survivors observed were similar to those expected to survive (82%) given typical survival rates for this species in Barcelona.

3.4.5 Natal philopatry and dispersal

The nests of 83 birds ringed as nestlings were located over the course of the study. Seven birds were first located during their second breeding season and were excluded because we could not be certain that their observed nest location was necessarily their first nest following dispersal. This left 76 birds for the study of natal dispersal and philopatry, 74 of which were sexed.

Thirty-one birds (41%) were philopatric to their natal tree, males (N = 24) being more likely to remain than females (N = 7). Six of these (3 males, 3 females) remained in the same chamber as at least one of their parents for the whole, or part of their first breeding season. Two males left their parents' nest chamber part way through their first breeding season, in both cases after being chased from the nest by parents during nest building and maintenance activities (one bird was observed being chased twice, the other bird was observed being chased four times). A further six males remained in the same nest as their parents, however they built their own nest chambers on to their parent's nest to form compound nests and made separate breeding attempts to their parents. These birds consisted of one trio of brothers, one dyad of brothers (see below) and an individual male. Four philopatric birds did not have marked parents, we could therefore confirm only that they were not sharing a nest chamber with individuals that could have been their parents (as these philopatric individuals were not sharing nest chambers with any unmarked birds). The remaining 15 birds built their own nests within their natal nesting trees entirely separate from their parents' nests. Forty-five of the 76 marked birds (59%; 17 females, 26 males and 2 unknown sex) dispersed to other nesting trees for their first breeding season.

Nineteen birds nested with a sibling (eight dyads of siblings and one trio) in their first year. For all but two of the dyads, we were able to confirm that the siblings nested with another bird, forming six trios and one group of four birds. The trio and four of the dyads of siblings were philopatric, nesting in their natal tree in their first breeding season; two of these groups used separate chambers in the same compound nest as their parents and the remaining four sibling dyads had dispersed to another tree as coalitions. The trio and seven of the dyads of siblings were all males, the remaining dyad was a male-female coalition and was one of the dyads that dispersed.

For all individuals, including philopatric birds and all members of sibling coalitions, median natal dispersal distance was 45 m (range = 0-1,795 m, mean = 158 m ± 310 SD, N = 76). The natal dispersal distance of females (median 144 m) was significantly further than that of males (median 15 m) when including all members of sibling coalitions (Z = - 2.44, N = 74, p = 0.015; Figure 3.4a). We also examined natal dispersal distances after removing one individual at random from each sibling pair and two individuals from the trio of siblings because these individuals (all males) were unlikely to have made independent choices on dispersal distance. In this more conservative dataset, median natal dispersal for all birds was 48 m (range = 0 – 1,795 m, mean = 145 m ± 258 SD, N = 66) and again the dispersal distance of females (median = 144) was significantly further than that of males (median = 16 m; Z = -2.44, N = 64, p = 0.015; Figure 3.4b). Removing the female from the male-female sibling pair rather than the male did not qualitatively change these results.

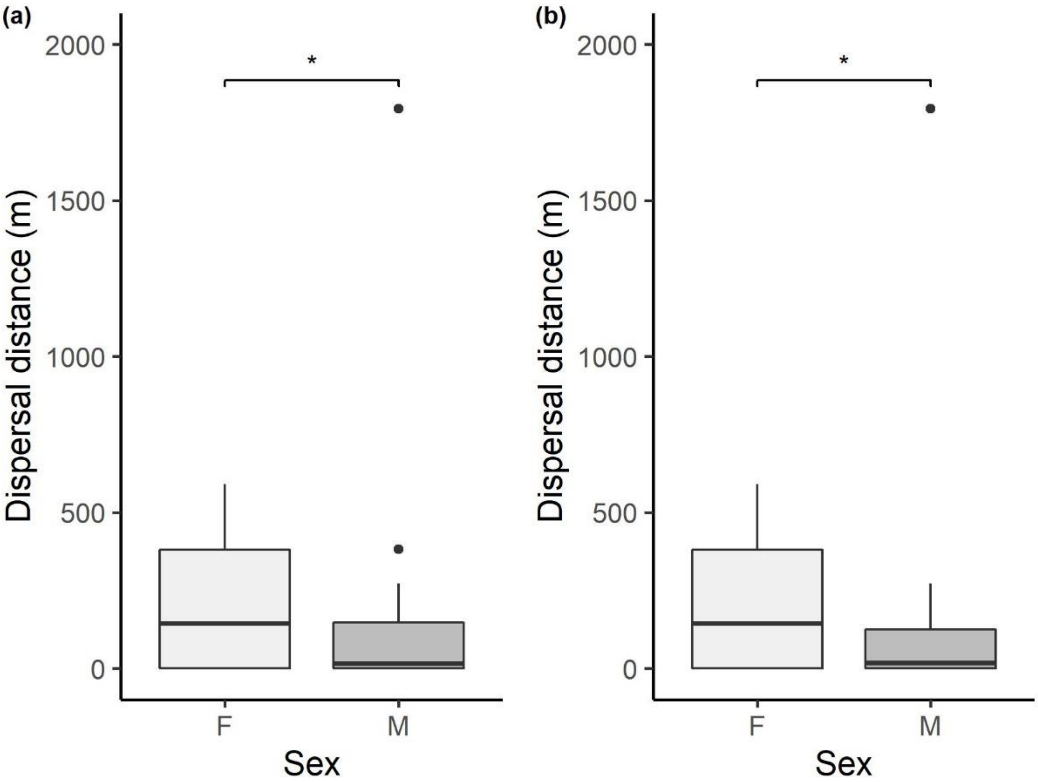

Figure 3.4. Natal dispersal distances for male and female monk parakeets including philopatric individuals; (a) all sexed individuals (males (M) N = 50, females (F) N = 24); (b) all sexed individuals excluding one/two birds from sibling coalitions (males N = 40, females N = 24). $*p < 0.05$. Boxplots indicate the interquartile range (box upper and lower limits), median dispersal distances (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

3.5 Discussion

Monk parakeets are unusual amongst parrot species in that they build their own stick nests that they use year-round for roosting and breeding (Eberhard, 1998; Forshaw, 1989; Spreyer & Bucher, 1998). Their nests can contain a single nest chamber or several individual nest chambers used by different pairs or groups. Nests are often loosely aggregated in the same and neighbouring trees. Here, we used a combination of population genetic analyses and detailed field observations to examine genetic structure in the monk parakeet and determine the demographic mechanisms driving the observed kin structure in this highly unusual social system. Our results revealed significant fine-scale genetic structure in our study population, with positive spatial autocorrelation of pairwise relatedness estimates among birds occupying the same nesting tree. Relatedness was higher than expected for all birds, among males, among females and between the sexes, indicating that relatives of both sexes are spatially clustered within nesting trees. This pattern was observed among adult birds after the period of natal dispersal and was therefore not the result of recently fledged individuals causing a temporary increase in spatial genetic structure (Scribner & Chesser, 1993).

We also showed that male monk parakeets are more related to other males sharing the same compound nest than to the males occupying the rest of the same nesting tree. This result held when we removed both within chamber comparisons and when randomly selecting a bird from a multi-male chamber for comparisons with other birds in the compound nest. There was no significant difference between the relatedness of focal males to females sharing the same compound nest when compared to the females in the rest of the tree. This result may indicate individuals avoid sharing compound nests with close relatives of the opposite sex. The pattern of clustering of relatives found here in monk parakeet nesting trees and compound nests echoes that found in a wide variety of taxa, from the large communal nests of sociable weavers (van Dijk et al., 2015) and the coteries of bell miners, *Manorina melanophrys* (Painter, Crozier, Poiani, Robertson, & Clarke, 2000), to the communal nests of mound-building mice, *Mus spicilegus*, (Garza et al., 1997), and the nests and colonies of a wide variety of social insects (e.g. Bono & Crespi, 2008; Pirk, Neumann, Moritz, & Pamilo, 2001).

Such clustering of relatives can have diverse ecological, behavioural and evolutionary implications. Living or breeding near kin can result in fitness benefits in the absence of obvious cooperative behaviours, for example through increased reproductive success (Fowler, 2005; Pasenhu, Viitala, Marienberg, & Ritvanen, 1998) or offspring survival (Brown & Brown, 1993). The fine-scale relatedness revealed by our analyses also creates an opportunity for kin-selected cooperation to operate in the monk parakeet. Monk parakeets exhibit a range of apparently cooperative behaviours that may have been influenced by aggregations of kin. For example, cooperative breeding (Bucher et al., 1990), the use of alarm calls in predator defence (F.S.E.D.P. personal observation) and potentially other more 'cryptic' kin-directed behaviours, such as foraging or breeding associations (Hatchwell, 2010). Moreover, associating with kin in compound nests may allow for a variety of additional kin-selected benefits in monk parakeets. For instance, nest building is energetically expensive (Mainwaring & Hartley, 2013), and monk parakeets use and maintain nests year-round (Bucher et al., 1990), so the nest may represent a significant energetic investment. Initiating a new chamber on a pre-existing nest may be less energetically and temporally expensive than constructing a new nest with less structural support (Martín & Bucher, 1993). In addition, the nest structures themselves may help to reduce energy expenditure. Like the nests of sociable weavers (van Dijk et al., 2013), monk parakeet nests act as buffers against fluctuations in external temperature, and are particularly effective at thermoregulation in hot temperatures (Viana, Strubbe, & Zocche, 2016). This could reduce energy expenditure by both nestlings and adults to maintain body temperature within optimal limits (Viana et al., 2016). If larger, compound nests are more effective at thermoregulation, then allowing relatives to build new chambers onto existing nests may result in energetic benefits for both parties. A further benefit of sharing compound nests may come from a reduction in the time and energy costs of nest maintenance or defence due to the greater number of birds occupying the nest. There are, therefore, a variety of avenues for both direct and indirect benefits of sharing compound nests with relatives, so the benefits of philopatry may be highest when new chambers are built on to the existing parental nest.

In many social birds, particularly those that breed cooperatively, prolonged associations of relatives and hence genetic structure arises through delayed or limited dispersal (Ekman, Dickinson, Hatchwell, & Griesser, 2004; Woxvold, Adcock and Mulder, 2006). In such cases, members of one sex tend to disperse before breeding occurs so inbreeding risk is relatively low (Koenig & Haydock, 2004). In species with 'kin neighbourhood' social systems (e.g. Dickinson & Hatchwell, 2004; Koenig and Haydock, 2004; Preston, Briskie, Burke, & Hatchwell, 2013), genetic structure exists among adults even after the period of natal dispersal, leading to a risk of inbreeding (Dickinson, Akçay, Ferree, & Stern, 2016; Lee et al., 2010; Leedale et al., 2018; Lukas & Clutton-Brock, 2011) and an increased chance of kin competition (Moore et al., 2006; Platt & Bever, 2009). We found that adult male and female monk parakeets live in kin neighbourhoods, with adults within nesting trees significantly more related than expected by chance. However, despite this close nesting proximity of relatives of opposite sexes, opposite sex relatives did not commonly share nests and we did not detect significant inbreeding in our population. A similar situation exists in sociable weavers, where natal philopatry to the colony is high, but individuals disperse within the colony, effectively dispersing from the family group whilst remaining in the natal colony, a strategy that may help to mitigate the risk of inbreeding (van Dijk et al., 2015). This is similar to what we observed in monk parakeets, where despite observations of natal philopatry in both sexes, the majority (62%) of philopatric birds disperse from the natal nest to build a new nest within the same nesting tree but independent of parental nests (see below).

A passive mechanism of inbreeding avoidance, such as sex-biased natal dispersal, may substantially reduce the risk of inbreeding (Johnson & Gaines, 1990). However, we still detected significant genetic structuring between the sexes within nesting trees, indicating that such passive processes may be insufficient to remove the risk of inbreeding completely. In such cases, if inbreeding is sufficiently costly there may be selection for active mechanisms of kin discrimination, for example, via kin-recognition or avoidance of familiar individuals as mates (Leedale, Li, & Hatchwell, 2020; Sherman, Reeve, & Pfennig, 1997). The monk parakeet has extensive vocal learning capabilities (Forshaw, 1989), and signatures of individual identity have been detected (Smith-Vidaurre, Araya-Salas, & Wright, 2020) that may allow discrimination between familiar and unfamiliar individuals, or kin and non-kin. Recognition and association of close kin using vocal cues has been demonstrated in a variety of cooperatively breeding species (e.g. Crane et al., 2015; McDonald & Wright, 2011; Sharp, McGowan, Wood, & Hatchwell 2005), and it has been suggested that the same mechanism may also be used for active avoidance of close inbreeding in the long-tailed tit (Leedale et al., 2020b). Further study of vocal recognition in the monk parakeet in the contexts of both cooperation and inbreeding avoidance would be worthwhile alongside a detailed study into relatedness of monk parakeet pairs.

Our investigation of the demographic processes generating the observed genetic structure at the level of the compound nest and nesting tree revealed three mechanisms: high nest site fidelity of adults, limited natal dispersal and coordinated dispersal and nesting of siblings. First, we found high breeding site fidelity in adult monk parakeets, with 55-78% of birds remaining in the same nesting tree between years when taking annual survival probabilities into account. In July 2018, all nests were removed in our study site as part of an invasive species management strategy, which probably explains the lower site fidelity between 2018 and 2019. However, high breeding site fidelity (55%) was still observed after nest removal, showing that individuals remained faithful to nest sites despite significant disturbance. Incidentally, routine nest removal may also limit the size of compound nests at our study site; nests containing 60 chambers are seen in parts of the native range of monk parakeets (Burger & Gochfeld, 2005), but not in Barcelona. Larger compound nests develop over time, so regular nest removal is likely to limit the number of such nests. Site fidelity in this species was expected to be high because nests are used year round and maintaining the same nest is presumably less costly than constructing a new nest elsewhere. On the other hand, long-term occupancy of older or larger nests may incur the potential cost of increased parasite load (e.g. Brown, Roche, & Brown, 2017; Spottiswoode, 2007). The parasite load of monk parakeet nests during the breeding season is high (F.S.E.D.P. personal observation), and the number of parasites on adult monk parakeets increases with increasing population density (Mori et al., 2019), although no comparison of parasite density in relation to nest size has been conducted yet.

High site fidelity by breeding adults alone does not explain the existence of kin-structured populations. Rather, it must operate in combination with other traits that ensure prolonged association of relatives, such as limited and/or coordinated natal dispersal, both of which we observed here. Natal dispersal distances were short (median distances of 16 m for males and 144 m for females) despite survey areas covering 6 km from the natal ringing locations. Our natal dispersal distances are considerably shorter than those reported in the native range (median 1,230 m), but that estimate was based on just four individuals (Martín & Bucher, 1993). Long-distance dispersal over 100 km has also been detected in the invasive range using genetic data (Gonçalves da Silva, Eberhard, Wright, Avery, & Russello, 2010). Despite female-biased dispersal we found significant genetic structure both within and between sexes at the level of the nesting tree. This reflects a degree of natal philopatry in both sexes, with some one-year old birds remaining either in the same nest or nesting tree as their parents. Building a separate nesting chamber on to the nest of parents is one mechanism for the formation of compound nests, and explains why males in compound nests are more related to each other than to males in the rest of the nesting tree. Taken together, limited natal dispersal combined with high breeding site fidelity by adults provides a mechanism for the formation of kin structure in this species that is widespread among social animals (Rubenstein & Abbot, 2017).

Finally, we also detected coordinated dispersal of sibling coalitions. These were composed predominantly of male siblings, but also involved one male-female sibling dyad, showing that while male coalitions are the most common coalition type in monk parakeets, mixed-sex coalitions do also occur. Four of these coalitions dispersed to a different nesting tree, but five remained in their natal tree. Dispersal of sibling coalitions has been observed in a number of bird species, including the vinous-throated parrotbill (Lee, Lee, & Hatchwell, 2010b), brown jay, *Cyanocorax morio* (Williams & Rabenold, 2005) and Arabian babbler, *Turdoides squamiceps* (Ridley, 2012). The majority of such studies involve single-sex coalitions, for example all male coalitions in the brown jay (Williams & Rabenold, 2005) but mixed-sex coalitions have also been reported in a number of species (Lee et al., 2010b; Sharp et al., 2008). These observations contrast with the general expectation that dispersal dilutes kin structure and precludes opportunities for kin cooperation; instead, dispersing in kin coalitions presents opportunities for kin-selected cooperation and additional benefits of associating with kin post-dispersal. For example, in the long-tailed tit dispersal in kin coalitions allows helpers to direct their assistance towards relatives even after dispersal (Sharp et al., 2008). Our results indicate that dispersal does not preclude opportunities for kin-selected cooperative behaviour in the monk parakeet and that dispersal of sibling coalitions may maintain kin-structure without requiring natal philopatry.

In conclusion, we have presented evidence of fine-scale genetic structure in an invasive population of monk parakeets, with relatives of both sexes clustered within nesting trees and male relatives aggregated in compound nests. Such spatial aggregations of relatives provide an opportunity for fitness benefits through kin-directed cooperation in a variety of behaviours, but also increase the risk of kin competition and inbreeding, although we found no evidence that inbreeding actually occurs. We also identified the key demographic characteristics that lead to kin-structured populations. Our study is the first to define fine-scale population genetic structure in this highly unusual social system and has implications for the evolution of social behaviour, colony formation and cooperation in this species.

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3.6 Supplementary information for:

Fine-scale genetic structure reflects limited and coordinated dispersal in the colonial monk parakeet, *Myiopsitta monachus*

Table S3.1. Multiplexes of microsatellite loci. Including information regarding whether loci were used in analyses and any reasons for exclusion of markers. Hardy-Weinberg equilibrium (HWE).

Locus	Reference	Multiplex	Used in analyses	Reason for exclusion
Mmon02	*Dawson Pell et al. 2020*	1	Yes	NA
Mmon03	*Dawson Pell et al. 2020*	1	Yes	NA
Mmon04	*Dawson Pell et al. 2020*	1	Yes	NA
Mmon05	*Dawson Pell et al. 2020*	1	No	departed from HWE
Mmon14	*Dawson Pell et al. 2020*	1	Yes	NA
Mmon06	*Dawson Pell et al. 2020*	2	No	departed from HWE
Mmon07	*Dawson Pell et al. 2020*	2	Yes	NA
Mmon15	*Dawson Pell et al. 2020*	2	Yes	NA
Mmon16	*Dawson Pell et al. 2020*	2	Yes	NA
Mmon01	*Dawson Pell et al. 2020*	3	Yes	NA
Mmon09	*Dawson Pell et al. 2020*	3	Yes	NA
Mmon10	*Dawson Pell et al. 2020*	3	Yes	NA
Mmon11	*Dawson Pell et al. 2020*	3	Yes	NA
Mmon13	*Dawson Pell et al. 2020*	3	Yes	NA
TG03-002	*Dawson et al., 2010*	4	Yes	NA
TG05-046	*Dawson et al., 2010*	4	Yes	NA
CAM20	*Dawson et al., 2013*	4	Yes	NA
MmGT057	*Russello et al. 2007*	5	Yes	NA
MmGT071	*Russello et al. 2007*	5	Yes	NA
MmGT030	*Russello et al. 2007*	5	Yes	NA
MmGT105	*Russello et al. 2007*	5	Yes	NA
MmGT046	*Russello et al. 2007*	5	Yes	NA
MmGT060	*Russello et al. 2007*	6	Yes	NA
MmGT054	*Russello et al. 2007*	6	No	null alleles >10%
MmGT090	*Russello et al. 2007*	6	No	departed from HWE
MmGT012	*Russello et al. 2007*	6	No	departed from HWE

Table S3.2. Allele distributions across polymorphic microsatellite markers. Number of alleles recorded per microsatellite locus used in estimating genetic relatedness in monk parakeets, *Myiopsitta monachus*, observed allele size ranges and observed (H_O) and expected (H_E) heterozygosity.

Locus	Number of unique alleles	Observed size (bp)	H_o	H_E
Mmon02	13	141-179	0.83	0.86
Mmon03	12	227-267	0.86	0.86
Mmon04	12	220-243	0.88	0.83
Mmon14	10	142-166	0.80	0.75
Mmon07	17	193-225	0.84	0.89
Mmon15	12	130-176	0.81	0.86
Mmon16	6	141-161	0.56	0.59
Mmon01	7	177-201	0.79	0.77
Mmon09	6	136-150	0.60	0.57
Mmon10	5	92-101	0.79	0.75
Mmon11	8	153-181	0.81	0.83
Mmon13	5	122-138	0.77	0.71
TG03-002	2	121-123	0.31	0.30
TG05-046	2	325-327	0.16	0.16
CAM20	3	182-186	0.40	0.45
MmGT057	5	115-129	0.59	0.68
MmGT071	5	201-226	0.55	0.56
MmGT030	9	299-315	0.84	0.82
MmGT105	8	196-217	0.76	0.68
MmGT046	4	160-166	0.54	0.54
MmGT060	3	93-101	0.30	0.28
Mean	7.33	-	0.66	0.65

154 unique alleles in total observed. Based on data from 112 individuals. Observed (H_O) and expected (H_E) heterozygosity calculated in SPAGeDI v. 1.5 (Hardy & Vekemans, 2002).

S3. Spatial autocorrelation analysis

To determine whether patterns of genetic relatedness observed at the level of the nesting tree for males and all birds were driven mainly by male relatives clustering within compound nests we conducted additional spatial autocorrelation analyses in SPAGeDI v. 1.5 (Hardy & Vekemans, 2002), following the same methods described in the main text. We randomly selected a single male from each compound nest to be included in these additional analyses and excluded the other males in that compound nest from the dataset. This resulted in the exclusion of 15 males, giving a total sample size of 97 birds for the analysis of all birds (51 males, 46 females) and 51 males for the male only analysis.

Mean ± SE relatedness within nesting trees was 0.034 ± 0.01 for all individuals and 0.05 ± 0.01 for males with SE calculated by jackknifing over loci. In both analyses, pairwise relatedness within nesting trees was higher than expected by chance ($p < 0.001$; Figure S3.1; based on 20,000 data permutations). Significant genetic structuring was not found beyond the level of the nesting tree in either analysis. These results confirm that the significant genetic structure we observed at the level of the nesting tree in the initial spatial autocorrelation analyses was not just a function of male relatives aggregating in compound nests, but must also result from kin being clustered within nesting trees.

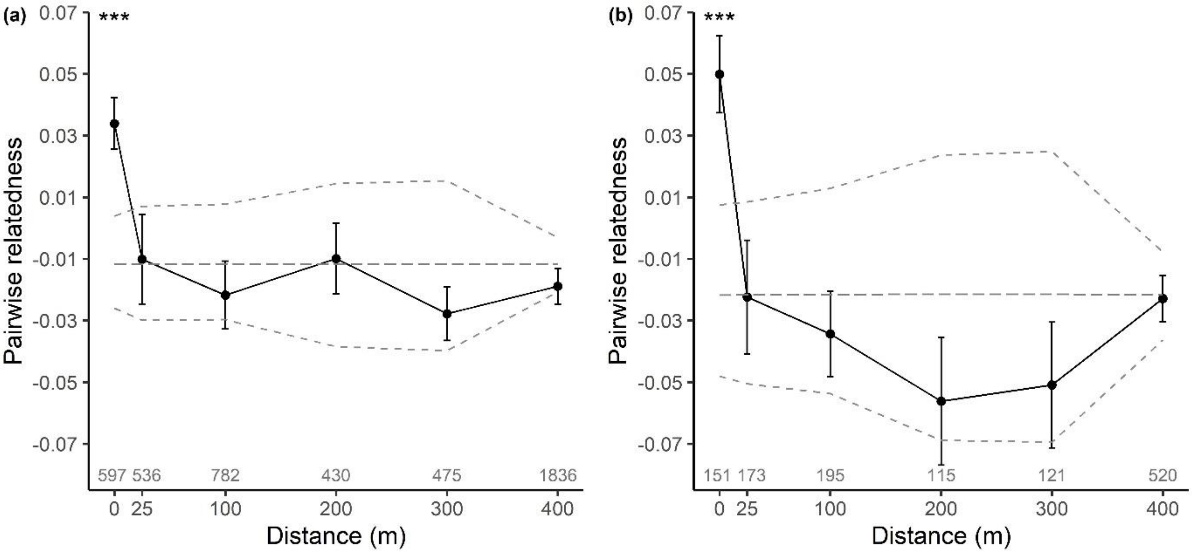

Figure S3.1. Mean pairwise relatedness ± SE within nesting trees (0 m distance) and over five further distance bands of inter-tree distances including only a single male from each compound nest: (a) among all individuals, (b) among males. Error bars generated by jackknifing over loci to approximate SE. Null mean pairwise relatedness and 95% CI generated through 20,000 data permutations indicated by dashed lines. Number of pairwise comparisons indicated above the x-axis for each distance band. ***$p < 0.001$.

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4. Ranging behaviour and habitat selection in an invasive bird

4.1 Abstract

Habitat selection has profound consequences for individual fitness. The natal habitat preference induction (NHPI) hypothesis proposes that individuals choose habitats that exhibit similar environmental cues to those experienced in early life. In this study, we first examined juvenile movements and dispersal, and tested the NHPI hypothesis in the monk parakeet, *Myiopsitta monachus*, an invasive species that nests primarily in pine or palm trees in our study site. Juveniles were observed ranging extensively, but we found no relationship between ranging distances prior to dispersal and subsequent natal dispersal behaviour. As predicted by NHPI, we found that dispersed individuals displayed a significant preference for nesting in their natal tree type in their first year, irrespective of tree availability. The probability of changing tree type was not influenced by individual dispersal distance, the proportion of the natal tree type available, or natal tree type. We found that adult birds undertaking breeding dispersal also showed a preference for the same tree type they dispersed from when making nest site selections, demonstrating that preferences can be maintained during breeding dispersal movements. Finally, conspecific breeding success did not differ between palm and pine tree nests, and so did not provide a useful source of public information regarding the suitability of the two nesting substrates. These results contribute to our understanding of the drivers of habitat selection in both adults and juveniles and have implications for our understanding of dispersal patterns and range expansion in this worldwide invasive species.

Keywords: Natal habitat preference induction, invasive species, monk parakeets, *Myiopsitta monachus*, breeding dispersal, ranging movements, public information, reproductive success.

4.2 Introduction

Habitat selection can have a profound influence on individual fitness and a multitude of ecological interactions (Hale, Treml, & Swearer, 2015; Huey, 1991; Thomson, Forsman, Sardà-Palomera, & Mönkkönen, 2006), so understanding the causes and the ecological and evolutionary consequences of individual variation in habitat selection is important (Davis & Stamps, 2004; Piper, Palmer, Banfield, & Meyer, 2013; Selonen, Hanski, & Desrochers, 2007; Tonnis, Grant, Grant, & Petren, 2005). One potential cause of individual variation in habitat choices is natal habitat preference induction (NHPI), which occurs when adults demonstrate a propensity to select habitats that exhibit similar environmental cues to their natal habitat (Davis & Stamps, 2004; Stamps & Davis, 2006). NHPI is an 'umbrella concept' that encompasses a range of connected terms and mechanisms of habitat preference including: natal habitat-biased dispersal, habitat imprinting and Hopkin's host selection principle (Davis, 2019; Mabry & Stamps, 2007). NHPI influences habitat selection in several taxa including insects (Lhomme, Carrasco, Larsson, Hansson, & Anderson, 2018), fish (Arvedlund, McCormick, Fautin, & Bildsøe, 1999), amphibians (Hepper & Waldman, 1992), reptiles (Roe, Frank, Gibson, Attum, & Kingsbury, 2010), mammals (Haughland & Larsen, 2004a; Merrick & Koprowski, 2016) and birds (Piper et al., 2013). NHPI has been implicated as a mechanism driving reproductive isolation and speciation (Tonnis et al., 2005; Beltman & Metz, 2005; Bolnick et al., 2009; Qvarnström & Vallin, 2011), and maladaptive habitat selection (Piper et al., 2013); it may also have conservation implications (Roe et al., 2010; Kleinstäuber, Kirmse, & Langgemach, 2018). However, conclusive demonstrations of NHPI in nature are few, perhaps due to the difficulty of assessing habitat availability in order to demonstrate a preference (e.g. Tordoff, Martell, & Redig, 1998).

In addition to their personal natal experience, individuals may use unintentional cues or deliberate signals from other individuals (social information) to select suitable territories or breeding sites (Boulinier & Danchin, 1997; Frederiksen & Bregnballe, 2001). Public information, a form of inadvertent social information, regarding the breeding success of conspecifics can influence the decisions that determine habitat choice (Boulinier & Danchin, 1997; Parejo, White, Clobert, Dreiss, & Danchin, 2007; Doligez, Danchin, & Clobert, 2002; Danchin, Boulinier, & Massot, 1998). For instance, in collared flycatchers, *Ficedula albicollis*, both settlement and departure decisions are influenced by conspecific breeding success (Doligez et al., 2002), and breeding-site selection has been experimentally influenced in the black-throated blue warbler, *Dendroica caerulescens*, using indicators of conspecific reproductive success (Betts, Hadley, Rodenhouse, & Nocera, 2008). In contrast, experimental manipulation of social information regarding indicators of reproductive success did not influence nest site choice by female wood ducks, *Aix sponsa*; instead, personal information about habitat structure appeared to affect decisions (Berg and Eadie 2020). The accessibility and reliability of information and the costs associated with obtaining it may influence the use of information from different sources (e.g. Danchin, Giraldeau, Valone, & Wagner, 2004; Kendal, Coolen, van Bergen, & Laland, 2005; Dunlap, Nielsen, Dornhaus, & Papaj, 2016; Van Bergen, Coolen, & Laland, 2004). For instance, public information may be particularly accessible in species that breed at high densities (Danchin et al., 1998), or may be of particular importance for naïve individuals with no personal breeding experience to draw from (Nordell & Valone, 1998). However, such information is likely to be more ephemeral than external habitat cues and therefore may be available to individuals over more limited timescales (Berg & Eadie, 2020).

Habitat selection is also influenced by exploratory behaviour and dispersal because these processes determine the habitats that individuals are able to sample before deciding where to settle. Dispersal behaviour is inherently difficult to study in open populations (Koenig et al., 1996). Moreover, studies routinely include dispersal outcomes but often report little regarding exploration behaviour pre-dispersal due to methodological, financial or time constraints. Nevertheless, several studies have shown that exploration behaviour typically occurs prior to dispersal (Cox & Kesler, 2012; Debeffe et al., 2013). Such exploratory forays may be related to, or even influence, dispersal behaviours, for instance, dispersal distance and direction may be influenced by distance and/or direction of exploratory movements (Haughland & Larsen, 2004; Debeffe et al., 2013). If exploration and dispersal are linked we may expect to observe sex differences in exploratory behaviour that reflect patterns of sex-biased dispersal, as observed in Florida scrub-jays, *Aphelocoma coerulescens*, (Sherer, 2019; Fitzpatrick, Woolfenden, & Bowman, 1999; Woolfenden & Fitzpatrick, 1984). Despite these demonstrations of exploratory behaviour in a variety of species, movements by pre-dispersal juveniles remains an understudied area of dispersal ecology and the potential ecological and evolutionary consequences warrant further investigation.

In this study, we use detailed field observations to investigate ranging behaviour, dispersal and the drivers of habitat selection in wild juvenile and adult monk parakeets, *Myiopsitta monachus,* an invasive parrot species native to South America (Forshaw, 1989), that has been introduced world-wide mainly through escapes from the pet trade (Bush et al., 2014; Lever, 2005; Russello et al., 2008). Unusually amongst parrots, monk parakeets are not cavity-nesters; instead they construct large stick nests that can contain many separate chambers and are used year-round for both roosting and breeding (Forshaw, 1989; Eberhard, 1998; Spreyer & Bucher, 1998). Multiple nests are often aggregated within trees (Bucher, Martin, Martella, & Navarro, 1990; Eberhard, 1998). Monk parakeets are non-territorial but will defend their nests from predators and conspecifics (F.S.E.D.P. personal observation). Previous investigations into dispersal behaviour revealed that natal dispersal is female-biased and dispersal occurs over relatively short distances in the urban environment (Dawson Pell, Senar, Franks, & Hatchwell, 2021); natal philopatry has also been observed in both sexes (Dawson Pell et al., 2021). However, little is known about movements by juveniles prior to natal dispersal or regarding the factors driving nest site selection in this species. Understanding patterns of habitat selection is particularly important for our understanding of invasion dynamics in the monk parakeet. Clear preferences for certain nesting substrates are shown in different locations around the world, despite the availability of suitable alternatives (e.g. Di Santo, Bologna, & Battisti, 2017; Roviralta & Garc, 2001) and preference for certain substrate types has been linked to large-scale range expansion in this species (Bucher & Aramburú, 2014). Therefore, understanding the drivers of nesting substrate preference during habitat selection by monk parakeets may help to predict dispersal and range expansions, key aspects of biological invasions.

In this study, we first investigated movements by recently fledged monk parakeets in the months post-fledging, testing whether ranging distances were related to whether an individual was philopatric in their first year post-fledging or dispersed, or to the sex of the individual. We also examined whether ranging distances were related to subsequent natal dispersal distances. We then examined evidence for NHPI and investigated the factors that may influence changes in nesting tree type. To the best of our knowledge, this is the first study to investigate NHPI in an invasive bird. In addition, we examined nesting tree type preferences following breeding dispersal by adult monk parakeets to determine whether preferences are maintained through breeding dispersal movements. Finally, we compared reproductive parameters in different tree types to examine whether conspecific productivity may be a useful source of public information regarding the suitability or quality of nesting tree types.

4.3 Materials and methods

4.3.1 Study site and species

The field study was conducted in the city of Barcelona, Spain (41.39°N 2.17°E) on the north-east coast of the Iberian Peninsula. The metropolitan area of Barcelona is approximately 102 km^2, comprising a highly developed urban environment with numerous parks containing both native and exotic vegetation. Barcelona has one of the highest densities of monk parakeets in Europe and the population is expanding exponentially (Postigo et al., 2019). In 2015, the population was estimated at 5000 birds (Molina, Postigo, Román-Muñoz, & Del Moral, 2016; Senar, Montalvo, Pascual, & Arroyo, 2017). Monk parakeet nests were first recorded in Barcelona in Ciutadella Park in palm trees, *Phoenix dactylifera*, in 1975 (Batllori & Nos, 1985) and in 1992 the first pine tree, *Pinus halepensis*, nests were detected (Sol et al., 1997). The vast majority of current nests in Barcelona are in palm

(68%) or pine (19%) trees, the focus of this study, with a small minority in other tree types (11% in 2015; J.C. Senar unpublished data). Nests in man-made structures (e.g. pylons; Newman et al., 2008) are reported elsewhere, but in Barcelona there are very few such nests (2%; J.C. Senar unpublished data).

4.3.2 Sample collection

Monk parakeet chicks were ringed during the breeding seasons (March-August) in 2003, 2017 and 2018, using a cherry picker to access nests. In 2003, chicks were ringed in Ciutadella Park, Passeig de Lluís Companys, Plaça de Tetuan and Jardins de Magalí. The same locations excluding Jardins de Magalí were used in 2017, and in 2018 nests were accessed only in Ciutadella Park and Passeig de Lluís Companys. Natal nesting tree type was recorded for each individual. For ringing, nestlings more than ~21 days old were removed briefly from nests and marked with aluminium leg rings and a unique medal on a neck collar (Senar, Carrillo-Ortiz, & Arroyo, 2012). Blood samples (maximum 50 µl) were extracted from either the jugular or brachial vein for genetic sex-typing (permit code: EPI/2015(01529/1498/2015). For details of blood sample storage, DNA extraction and PCR protocols see Dawson Pell et al., (2020). Blood samples were unavailable for the juveniles that fledged in 2003, but all other ringed juveniles included in analyses ($n = 56$) were sexed using a sex marker, Z002B (Dawson, 2007), previously confirmed to sex monk parakeets successfully (Dawson Pell et al., 2020).

4.3.3 Compliance with ethical standards

Monk parakeets were handled and blood samples extracted with special permission EPI 7/2015 (01529/1498/2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan regional ethical guidelines for the handling of birds. JCS received special authorization (001501-0402.2009) for the handling of animals in research from Servei de Protecció de la Fauna, Flora i Animal de Companyia, according to Decree 214/1997/30.07.

4.3.4 Juvenile movements

To investigate habitat sampling by juvenile monk parakeets prior to dispersal and to validate our method of using the mean dispersal distance to assess tree availability (see *Nesting tree selection following natal dispersal*), we used data collected for a concurrent study into social associations and foraging behaviour of monk parakeets (F.S.E.D.P. personal observation). We collected data in the months following fledging (June-September) in 2017 and 2018. These data were collected in three ways: either by observations conducted for approximately three hours every week at an artificial food source (containing sunflower seeds and peanuts) set up on the roof of the Museu de Ciències Naturals de Barcelona within Ciutadella Park, or opportunistic recording of the location of individuals encountered during surveys of the core field site in Ciutadella Park or during surveys across the city of Barcelona. The majority of observations of individuals were made during surveys of Ciutadella Park, however, surveys of sites of up to 6 km from the main study area were made. Monk parakeets are non-territorial, so for this study we defined ranging movements as any movements away from the nesting tree by recently fledged individuals; such ranging movements may include foraging trips as well as more exploratory forays to assess habitat.

We calculated distances travelled by the juveniles using the GPS coordinates of the sighting location and the natal tree and the distGeo function in the geosphere package (Hijmans, Williams, & Vennes, 2019). In these analyses we included birds that were philopatric and those that dispersed for their first breeding season. Out of 73 possible individuals we observed 67 of these birds away from their natal tree in the months following fledging with a total of 509 observations. The number of sightings per individual ranged from one to twenty-seven (mean ± SD; 7.6 ± 6.1 observations). We examined both the observed mean and maximum distance an individual travelled from their natal tree. Mean observed distances travelled by juveniles ranged from: 3 - 994 m (mean ± SD; 148 ± 151 m), and maximum distances ranged from 3 - 1587 m (mean ± SD; 305 ± 256 m). These data indicate extensive movements by recently fledged juveniles and suggest any significant findings related to tree type selection would not be the result of limited habitat sampling. Based on these ranging distances of recently fledged juveniles, we deem it appropriate to use the mean dispersal distance of individuals to calculate the availability of tree types to each bird as this is within the distances travelled by recently fledged birds (see *Nesting tree selection following natal dispersal*).

To examine whether mean or maximum observed ranging distances were influenced by the sex of the individual or the number of observations of each bird we constructed separate generalised linear models (GLM) with Gaussian error distributions in R version 3.5.0 (R Core Team, 2018). We checked model assumptions and transformed data where required. The response variables, mean and maximum distance from the natal tree, were log-transformed and square-root transformed respectively and we included sex and the number of observations per individual as predictor variables. We considered terms significant at $p < 0.05$. We also tested for differences in the mean and maximum ranging distances of individuals that dispersed or were philopatric in their first year post-fledging using a Wilcoxon rank sum test and a t-test on square-root transformed data respectively. For this analysis, and all other occasions in this study, we define philopatric behaviour as birds that remained nesting in their natal tree for their first breeding season post-fledging; birds that nested any distance from their natal tree were considered to have dispersed.

To examine the relationship between dispersal distances and either the mean or maximum ranging distance we conducted separate linear regressions. We also investigated whether either dispersal or maximum recorded ranging distance was further for each individual.

4.3.5 Nesting tree selection following natal dispersal

The nest locations of marked monk parakeets were recorded in the breeding season of their first year post-fledging (2004, 2018 or 2019) during surveys of nests in Ciutadella Park and nest sites elsewhere across Barcelona. Over 640 hours were spent surveying the main colonies across Barcelona, up to 6 km from Ciutadella Park (2004: 260 hours (Carrillo-Ortiz, 2009); 2018 and 2019: 387 hours). When marked birds were located, the tree type and GPS coordinates of the nest were recorded. Individuals were recorded as nest occupants only if they were seen either in a nest chamber or delivering nest material; birds observed only perched in a tree containing a nest were not assumed to occupy a nest in that tree. All statistical analyses were performed in R version 3.5.0 (R Core Team, 2018). Dispersal distances were calculated using the distGeo function in the geosphere package (Hijmans et al., 2019) using GPS coordinates of natal and first year nesting trees.

The nests of 103 birds we ringed as nestlings were located during the study. A number of birds were excluded from the data set; seven birds were first located during their second breeding season and were excluded because experience during their first breeding season may have influenced subsequent nest location. Three birds that nested in tree species other than palms or pines were also excluded. Twenty-one birds (nine dyads, one trio) had built nests with siblings and could not be considered independent, so one bird from each dyad and two birds from the trio were removed before analyses. Thirty-three of the one-year-old birds nested in their natal tree; five of these (two males, three females) remained in a nest chamber with at least one parent bird and were excluded for not having chosen where to place their own nest. The other twenty-eight philopatric birds (four females, twenty-one males, three unknown sex) had paired and built their own nests in their natal tree and were not excluded from initial analyses. Some birds fell into more than one exclusion category.

We first examined whether birds were more likely to be philopatric when fledging from a pine or palm tree using a chi-square test of independence. For this analysis we had 78 individuals. To be conservative, we then excluded any philopatric birds from the analysis of NHPI, because philopatry may have dictated their nest tree choice. Following these strict exclusion criteria, we had 56 birds (24 males, 18 female, 14 unknown sex) in a conservative data set for analyses of NHPI.

The availability of tree types for nesting was determined using the tree inventory managed by Barcelona City Council containing data from the entire city (Open Data Barcelona). Mean dispersal distances for juveniles was 386 m when philopatric birds were excluded (see *Results*), and we used this distance as a proxy for average search distance to determine the numbers of each tree type likely to be encountered by individuals. This distance was well within maximum observed ranging distances of individuals (see *Results*). Using QGIS version 3.4.14 (QGIS Development Team, 2018) we created 'search areas' for each individual as circles with a radius of 386 m with the natal tree at the centre of the circle and determined the number of each tree type available within this search radius. Included in the palm tree count are *Phoenix dactylifera* and *Phoenix canariensis,* both of which are used by monk parakeets for breeding, and pine trees included *Pinus brutia, P. halepensis, P. nigra, P. pinaster, P. pinea and P. roxburghii*, all of which may be used by parakeets for nesting. All but three birds had both pine and palm trees available to them within the exploration radius. Three birds that fledged in 2003 had only palms available, having fledged from palm nests that were 595 m, 624 m and 657 m from their nearest pine tree. The number of palms available to birds within the search radius ranged from 12 to 150 (mean ± SD; 120 ± 39) and the number of pines ranged from 0 to 251 (mean ± SD; 52 ± 48). For each individual we calculated the proportion of available pines and palms within the 386 m radius. All trees were assumed to be available for nesting because many nests can be constructed in a single tree, therefore occupied trees are still available for settlement by newcomers.

In our assessment of vegetation availability we used a fixed search radius, however, individual differences in dispersal distances have the potential to alter the habitat available to dispersers (Mabry & Stamps, 2007), therefore we also examined whether the dispersal distance of an individual influenced the probability of an individual changing tree type. We ran a binary logistic regression generalised linear model (GLM) with a logit-link function including the binary response variable; whether an individual changed tree type. Using this model, we investigated the possibility that the proportion of the natal tree type available within the assigned search radius (386 m), the natal tree type, the interaction between the natal tree type and the proportion of the natal tree type available, the dispersal distance of an individual, or the interaction between natal tree type and dispersal distance influences the probability an individual changes tree type. We checked model assumptions and transformed data where necessary. We conducted model reduction through stepwise backwards elimination (Crawley 2005); comparisons of models were conducted using likelihood ratio tests and terms were removed by order of least significance. P values for removed terms were calculated by comparisons between the minimal model without the term included and a model including the term. Final significance values for retained terms were obtained by comparing the minimal model with a model from which the term of interest was removed.

4.3.6 Nesting tree selection following breeding dispersal

We examined whether adult birds undertaking breeding dispersal demonstrated a preference for nesting in the same nesting substrate they had previously used following dispersal movements. For this investigation, we used data collected for a concurrent study on monk parakeet population genetic structure and dispersal behaviour (Dawson Pell et al., 2021). We used data from 25 breeding dispersal events by adults to examine vegetation preference for individuals that dispersed between breeding seasons. For this investigation, all birds we observed undertaking breeding dispersal movements dispersed from pine trees (for details of surveys etc. see Dawson Pell et al., 2021). We examined nesting tree type following breeding dispersal for each dispersal event. Using the same search distance (386 m) we applied for juveniles, we assessed the available vegetation for each bird that underwent breeding dispersal. This distance is within reported home range sizes (radius 300-400 m) for adult monk parakeets (Carrillo-Ortiz, 2009) and also within reported breeding dispersal distances at our study site (max. 464 m recorded; Dawson Pell et al., 2021). As with birds in the natal dispersal analysis, for each individual we calculated the proportion of available pines and palms within the 386 m search radius. Mean proportion of palm trees when including data for all birds was 0.75 (range: 0.49-0.89) and the mean proportion of pines was 0.24 (range: 0.1-0.51). Due to small numbers in one category we were unable to perform a binary logistic regression as above as this prevented model convergence. Alternatively, we applied two chi-square tests, one test assuming the most abundant tree within each individual's assigned search radius was selected to generate expected numbers of individuals selecting each tree type and one test using the mean tree abundance to generate expected numbers.

4.3.7 Breeding success

In addition to, or instead of, personal information, individuals may use public information regarding conspecific breeding success in the process of nest site selection. In order to assess the potential for this to occur we compared reproductive success in pine and palm tree nests at our study site. Breeding activity was monitored from April-June (first broods) 2017 in Ciutadella Park and the Passeig de Lluís Companys, accessing nests with a cherry picker. During each nest chamber check, we recorded whether it was being used for breeding, the clutch size, and the number and age of any chicks present (estimated from known monk parakeets growth rates; Carrillo-Ortiz, 2009). Each active nest was visited 2 or 3 times over the course of the first brood and we assumed that any chicks that attained ringing age (> ~21 days) fledged successfully. Approximately half of monk parakeet pairs in Barcelona attempt a second brood, but clutch size, and fledging success are significantly lower in second broods (Senar et al., 2019), and due to fieldwork constraints we were unable to continue nest monitoring and ringing of chicks over the course of the second brood so in this study we focus only on reproductive success in first broods. We used Wilcoxon rank sum tests to investigate whether clutch size or the number of fledglings differed between nests in pine and palm trees.

4.4 Results

4.4.1 Juvenile movements

There was a significant positive correlation between the mean and maximum observed ranging distances (r_s = 0.756, n = 67, p < 0.001; Figure S4.1). We used the locations of observations of post-fledging juveniles to determine whether their ranging behaviour determined subsequent dispersal distance. We observed more males (N = 45) away from the nest than females (N = 22), however the number of sightings per individual (mean ± SD; 7.6 ± 6.1; N = 67) did not differ between males (mean ± SD; 8.4 ± 6.2) and females (mean ± SD; 5.9 ±5.6; Wilcoxon rank sum test; Z = -1.869, p = 0.062).

Neither the sex of the individual observed (Figure S4.2), nor the number of sightings of an individual was significantly related to either the mean or maximum observed ranging distance (Table 4.1).

Table 4.1. GLM examining factors affecting mean and maximum observed ranging distances of juvenile monk parakeets

Model	Parameter	Estimate ± SE	t	p
Mean ranging distance	(Intercept)	1.951 ± 0.113	17.240	<0.001
	Sex	0.088 ± 0.123	0.718	0.476
	Number of sightings	-0.004 ± 0.010	-0.380	0.705
Maximum ranging distance	(Intercept)	13.056 ± 1.696	7.698	<0.001
	Sex	1.988 ± 1.838	1.081	0.284
	Number of sightings	0.213 ± 0.142	1.494	0.140

N = 67 birds (22 female, 45 male). Mean ranging distance was log-transformed and maximum ranging distance was square-root transformed.

Neither the mean nor the maximum ranging distances differed between birds that dispersed (N = 37) and birds that were philopatric (N = 30) in their first year post-fledging (mean: Z = -1.437, p = 0.151; maximum: t = 0.912, p = 0.365; Figure 4.1).

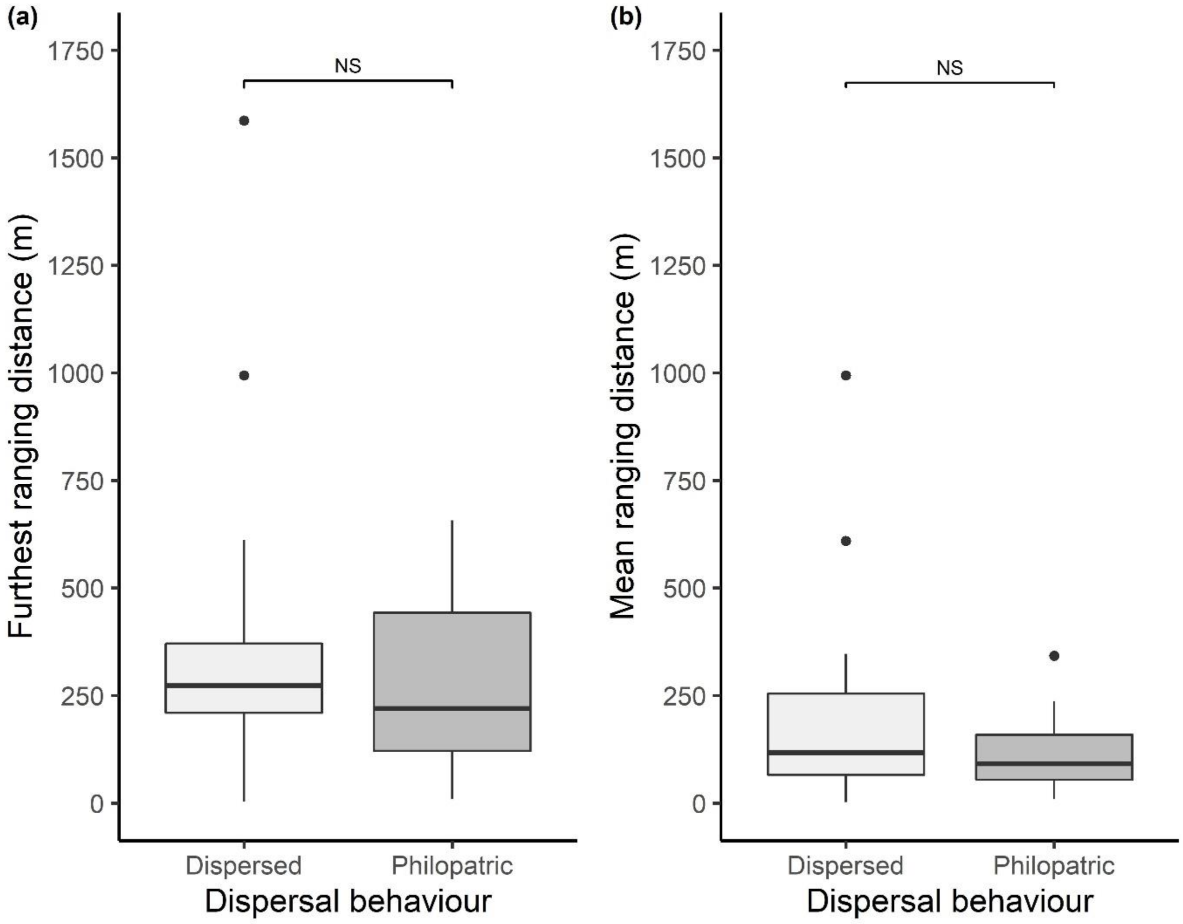

Figure 4.1. a) Maximum and b) mean ranging distances of juvenile birds that dispersed for their first breeding season (N = 37) compared to birds that were philopatric in their first season (N = 30). All data recorded in the months post-fledging (June-September). Boxplots indicate the interquartile range (box upper and lower limits), median dispersal distances (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

Both dispersal and ranging distances were available for 34 individuals. Dispersal distance was not related to either the mean (linear regression: $F_{1,32} = 0.992$, N = 34, $R^2 = 0.030$, p = 0.327) or the maximum ranging distance ($F_{1,32} = 1.408$, N = 34, $R^2 = 0.042$, p = 0.244), indicating that birds that moved greater distances from the nest in the months post-fledging do not also disperse greater distances. For 20 out of these 34 birds (59%), the maximum observed ranging distance exceeded dispersal distance, indicating that birds readily ventured further than they dispersed in the urban environment.

4.4.2 Nesting tree selection following natal dispersal

Birds fledging from pine trees were more likely to be philopatric to the natal tree than birds fledging from palm trees ($\chi^2 = 5.5$, $p = 0.019$; Figure 4.2).

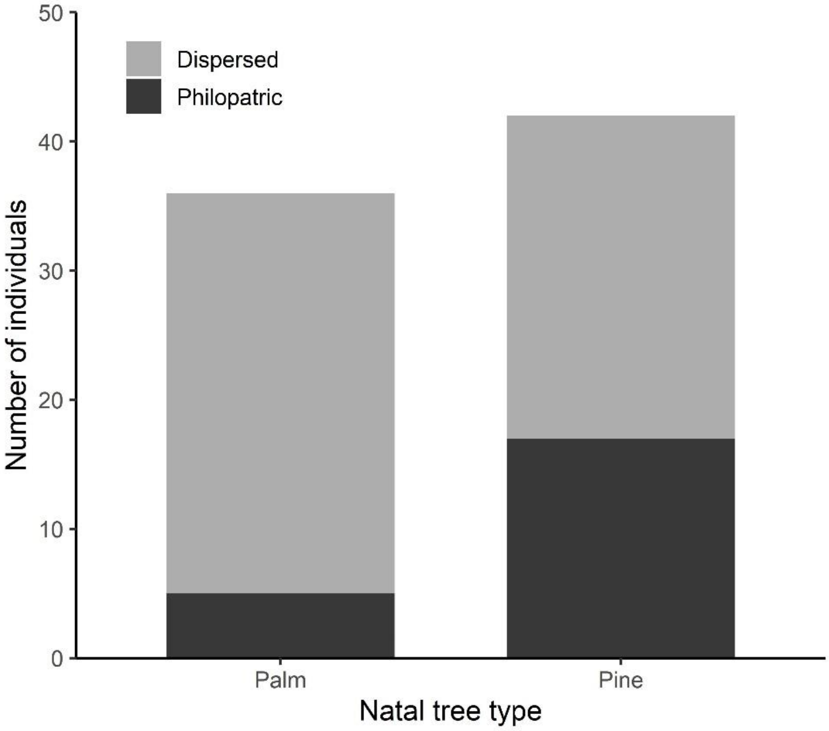

Figure 4.2. The number of individuals fledging from pine and palm trees that were philopatric to their natal tree or dispersed for their first breeding season. N = 78.

For birds that were not philopatric to their natal tree, we found a significant preference for the natal tree type (intercept $p < 0.05$; Table 4.2) and this effect was stronger for birds fledging from palm trees compared to pine trees ($p < 0.05$ Table 4.2). The probability of changing tree type was not significantly influenced by the proportion of the natal tree type available, the interaction between the proportion of the natal tree type available and the natal tree type itself, the interaction between log(dispersal distance) and the natal tree type, or log(dispersal distance) (all $p > 0.05$; Table 4.2).

Table 4.2. Correlates of the probability of changing tree type (N = 56; 24 male, 18 female, 14 unknown sex). Parameter estimates (β), standard error (SE), z and p-values for binary logistic regression models.

Parameter	β	SE	z	p
Intercept	4.011	± 1.685	2.381	0.017**
Natal tree type	-1.524	± 0.659	-2.313	0.015**
Log(dispersal distance)	-1.129	± 0.638	-1.771	0.064*
Proportion natal tree				*0.564*
*Proportion natal tree*Natal tree type*				*0.828*
*log(dispersal distance)*Natal tree type*				*0.246*

We present information on terms in the final models and those removed through stepwise backwards elimination. Terms were retained at p < 0.1. *p < 0.01, **p < 0.05. Dropped terms indicated in italics. Effect sizes (± SE) were obtained from the minimal model in each case. We individually returned dropped terms removed during model selection to the minimal model to assess significance using likelihood ratio tests, where appropriate also including individual terms from the interaction in this assessment.

4.4.3 Nesting tree selection following breeding dispersal

We observed 25 breeding dispersal events by 24 adults in the study area, all of which involved birds that dispersed from pine trees (Dawson Pell et al., 2021). Eight (33%) of these were by individuals marked as nestlings in 2017, five used the same tree type in their first breeding season as their natal tree type and the other three changed tree type for their first breeding season. When these eight individuals undertook breeding dispersal, seven used the same tree type following dispersal and the remaining bird changed tree type, reverting to its natal tree type. Of the total of 25 breeding dispersal events, 23 (92%) involved birds moving from one pine tree to another pine tree, and 2 (8%) birds moved from a pine tree to a palm tree. Birds were significantly more likely to select the same tree type as the one they were dispersing from for their new nest, despite the availability of the alternative tree type, when we used the most abundant tree type to generate expected choices (pine: $\chi^2 = 239.7$, $p < 0.001$; Figure 4.3a) and when we used overall proportions of vegetation to generate expected numbers of birds nesting in each tree type ($\chi^2 = 63.4$, $p < 0.001$; Figure 4.3b).

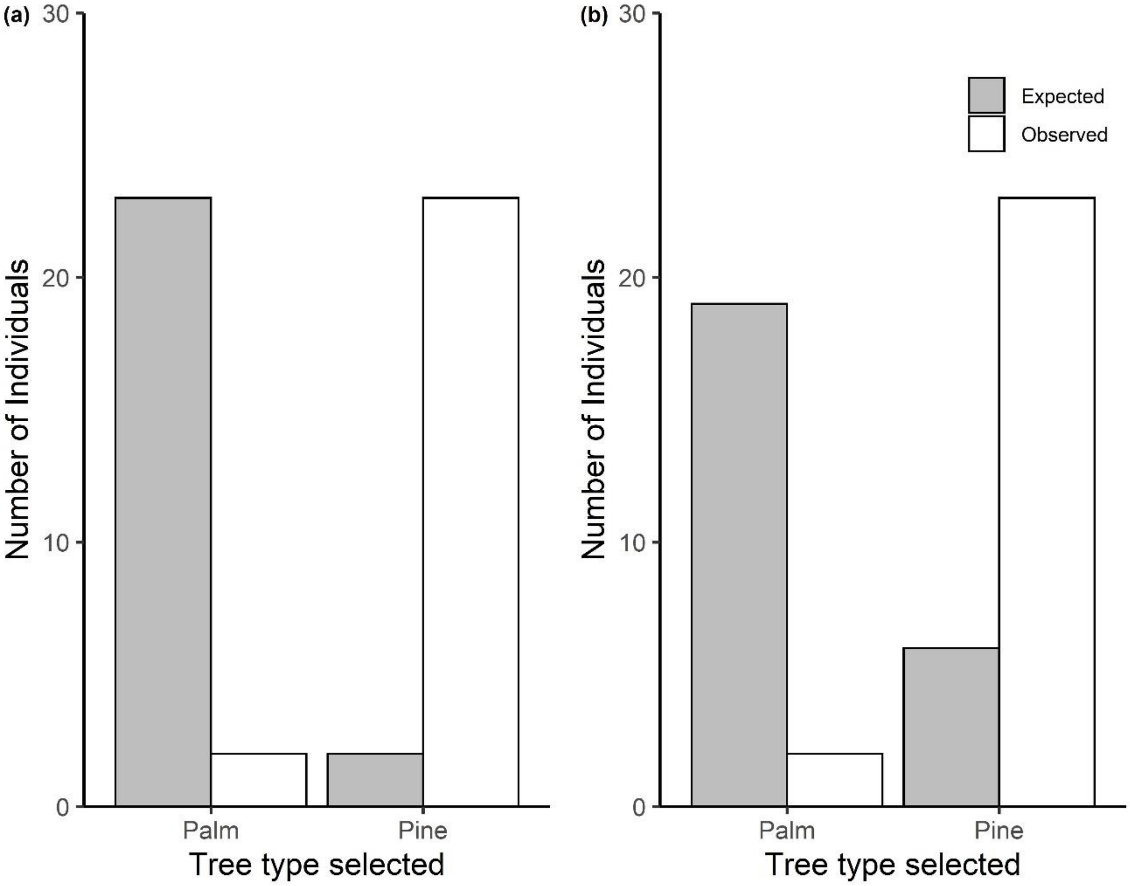

Figure 4.3. Breeding dispersal tree type selection by adult monk parakeets (N = 25 breeding dispersal events). Observed and expected values for tree type selection shown for a) expected values calculated by assigning the expected tree type per individual based on abundance within an individual's 386 m search radius ($p < 0.001$) and b) expected values calculated using the mean proportions of available vegetation ($p < 0.001$).

4.4.4 Breeding success

We monitored breeding success in 23 palm trees containing 23 nests and 40 separate breeding chambers, and ten pine trees containing 41 nests and 49 breeding chambers. There was no significant difference between palm and pine trees in either clutch size (Z = - 0.996, p = 0.32; Figure 4.4a) or the number of fledglings (Z = -0.564, p = 0.57; Figure 4.4b).

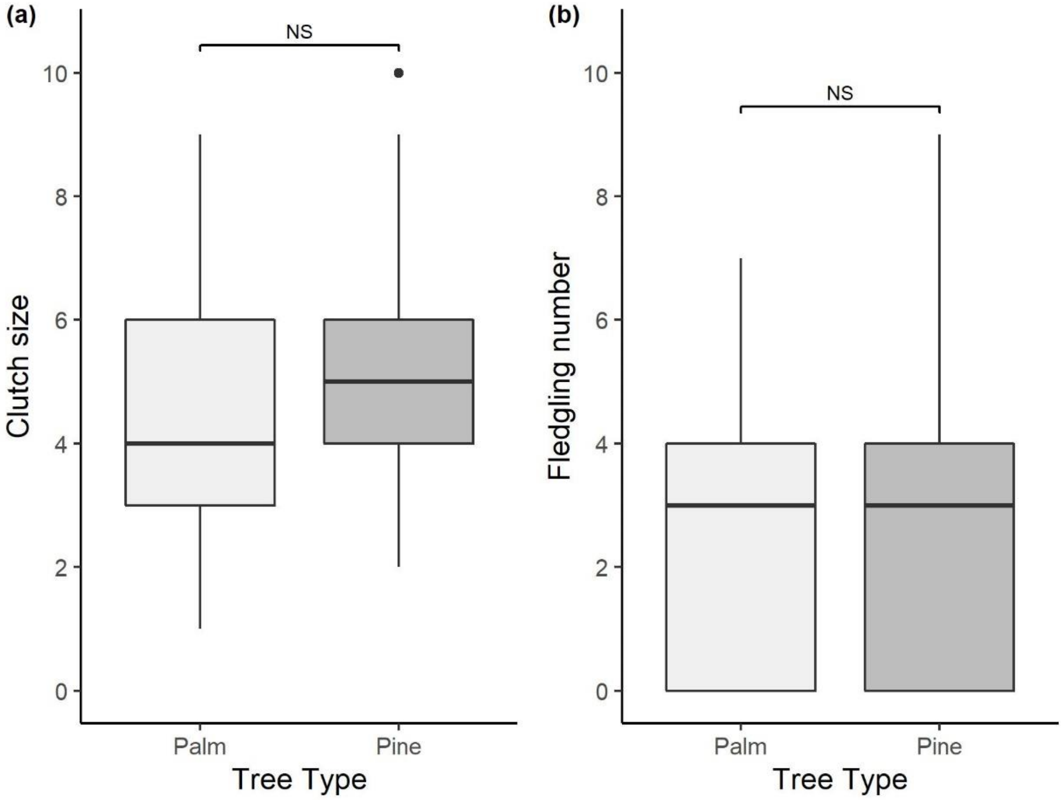

Figure 4.4. Breeding success in palm and pine trees: (a) clutch size, (b) fledgling number (>c.21 days old assumed to have fledged). Boxplots show interquartile range (box upper and lower limits), median values (dark lines within boxes), maximum and minimum values excluding outlier (lines extending from boxes) and outlier (dot).

4.5 Discussion

Monk parakeets were significantly more likely to select their natal tree type in their first breeding season, rather than change tree type, regardless of the availability of the nesting substrates. This result provides evidence for NHPI, a phenomenon rarely demonstrated outside a laboratory environment. These results add to a growing body of evidence suggesting NHPI may be a common mechanism for habitat selection (e.g. Merrick & Koprowski, 2016; Piper et al., 2013; Selonen et al., 2007). We confirmed that the proportion of the natal tree type available within the search radius did not significantly influence the probability of changing tree type between natal and first breeding seasons supporting our finding that birds exhibited a preference that was independent of substrate availability.

Where NHPI has been demonstrated in nature, the availability of alternative habitat types has not always been taken into account (e.g. Tordoff et al., 1998). Palm and pine trees are widely distributed across Barcelona and both tree types were available to all but three individuals in our study within the assigned search area. In addition, we demonstrated extensive ranging movements by recently fledged monk parakeets and adult birds have been previously shown to routinely travel hundreds of metres and even several kilometres to forage (Carrillo-Ortiz, 2009; Senar, Domènech, Arroyo, Torre, & Gordo, 2016), so our results cannot be attributed to limited vegetation availability or habitat sampling.

There are a number of hypotheses as to why NHPI as a mechanism for habitat selection may have adaptive significance (Davis & Stamps, 2004). NHPI may be selected for if it enables individuals to effectively and quickly discern high quality habitat (Davis, 2019; Davis & Stamps, 2004). As habitat enabling the rearing of offspring to independence is likely to be of sufficient quality (Stamps, Luttbeg, & Krishnan, 2009), settling in habitats that exhibit similar stimuli to natal habitats may reduce the costs associated with habitat assessment and hence reduce dispersal risks, a process termed ‘habitat cuing’ (Davis & Stamps, 2004; Stamps, 2001; Wauters, Verbeylen, Preatoni, Martinoli, & Matthysen, 2010). Alternatively, experience accrued in the natal habitat may improve an individual’s performance in similar habitats post-dispersal. This is termed ‘habitat training’ and can refer to any morphological, physiological or behavioural change (Stamps, 2001; Stamps & Davis, 2006). Juvenile monk parakeets frequently delay dispersal, often for many months (Martín & Bucher, 1993; Emlen, 1990) providing ample opportunity to learn nest-building techniques appropriate for their natal tree type. Building techniques are likely to differ between trees; pine tree nests are often constructed around thin, densely packed branches, whereas palm tree nests are built with much more structural support from the bases of palm fronds. Therefore, birds may be more efficient when building their own nest in the same tree type as their natal nest. However, this hypothesis remains untested.

NHPI is considered to be a learned preference for cues from the natal habitat, however, it is possible preferences could be heritable (Jaenike & Holt, 1991). Without addressing the possibility for an inherited genetic preference driving habitat selection in the monk parakeet, we have not demonstrated NHPI *sensu stricto*, but a cross-fostering experiment could be employed to address this, as suggested for previous study systems in which NHPI has been demonstrated without directly addressing the issue of heritable preferences (e.g. Piper et al., 2013).

Monk parakeets showed a marked preference for building new nests in pine trees when undergoing breeding dispersal from pine trees, indicating that a preference for this nesting substrate is maintained through the process of breeding dispersal. Although we are not able to disentangle whether this is a maintained natal preference or perhaps the result of preference driven by personal breeding experience, the majority of these breeding dispersal events (84%) occurred following nest destruction as part of an invasive species control programme (Dawson Pell et al., 2021). Nest destruction and any consequential loss of reproductive success could influence dispersal decisions. For instance, northern flickers, *Colaptes auratus*, disperse further following nest predation than following a successful nesting attempt (Fisher & Wiebe, 2006) and breeding failure in black kites *Milvus migrans* leads to breeding dispersal in both sexes (Forero, Donázar, Blas, & Hiraldo, 1999). However, despite nest destruction, individuals were still highly faithful to the nest site (Dawson Pell et al., 2021) and the vast majority (90%) that did disperse moved to the same tree type, indicating that reproductive failure, or significant disturbance of nesting sites did not influence preferences for nesting in pine trees. It is worth noting that nest destruction in this instance occurred after the first brood and at the start of the second brood, so birds may have fledged a successful first brood before nest destruction. Our results may point to long term preferences for the natal tree type, in this case pine trees only, and may indicate that NHPI could have long-term consequences for fitness or mate choice in this species. It should also be noted that we did not follow the majority of birds from fledging so we had no data on whether they had previously changed tree type and now demonstrated an alternative preference. A maintenance of natal preference could be confirmed by longer term investigations into nesting tree preference over multiple breeding seasons.

Despite female monk parakeets demonstrating a greater propensity to disperse and dispersing further (Dawson Pell et al., 2021), this pattern was not reflected in the ranging distances of individuals with both males and females observed at similar mean and maximum distances from their natal nests at our study site in the first four months post-fledging. North American red squirrels, *Tamiasciurus hudsonicus*, also exhibit no sex difference in exploration distance (Haughland & Larsen, 2004), but our results contrast with the exploratory forays of Florida scrub-jays, in which sex differences in exploratory distances echo patterns of sex-biased dispersal (Sherer, 2019; Fitzpatrick et al., 1999; Woolfenden & Fitzpatrick, 1984). In addition, the movements we observed in the monk parakeet were not related to whether an individual dispersed or was philopatric in their first year. This result is similar to that observed in the flying squirrel, *Pteromys volans* (Selonen & Hanski, 2006), but contrasts with the pattern of exploratory forays in roe deer, *Capreolus capreolus*, in which individuals that dispersed explored more than those that remained philopatric (Debeffe et al., 2013). It is possible that the distances moved by juvenile monk parakeets increase or change over time, so the movements we recorded in the first four months post-fledging may not have captured exploratory behaviours most relevant to dispersal that may occur prior to the onset of the first breeding season. It should also be noted that our estimates of ranging distances included all movements away from the nesting tree, including foraging trips as well as potential exploratory forays. Indeed, there may be no clear distinction between the two kinds of movement in a non-territorial species where home ranges may be very large and overlap extensively with conspecifics. However, the important point is that whether movements were made for habitat exploration or for foraging we have shown that monk parakeets routinely travel distances that exceed dispersal distances, and therefore that birds have ample opportunity to sample habitat beyond that selected as a nest site.

We also tested whether public information regarding relative breeding success in pine and palm trees may be useful during the process of nesting tree selection. The prolonged breeding season of monk parakeets in Spain (two broods, 6-7 months; (Senar et al., 2019)) would likely allow for assessment of conspecific breeding success because fledged birds roost in their natal nest post-fledging and are regularly fed by adults at the nest and are therefore visible to prospecting individuals (F.S.E.D.P. personal observation). Moreover, colonial behaviour facilitates the use of public information (Brown, Brown, & Danchin, 2000; Danchin et al., 1998) and such public information may be particularly useful for naïve individuals with no personal experience of breeding (Nordell & Valone, 1998). However, productivity did not differ between pine and palm trees, at least for first broods, so if public information is used, it would indicate that these substrates are equally suitable for nesting. To further address the possibility that public information influences nest site choice in the monk parakeet, experimental manipulation of breeding success and subsequent monitoring of habitat selection, and assessments of offspring quality and recruitment could shed more light on the salient cues used during habitat selection in this species.

Our results are consistent with patterns of nesting substrate use by monk parakeets across their native and invasive range. Nesting substrates vary between locations, but within each location certain substrates are used consistently despite the availability of alternatives. For example, cedars, *Cedrus spp*, are preferred in both Rome (Di Santo et al., 2017) and Madrid (Roviralta & Garc, 2001), while man-made structures, such as electricity substations, are often used in North America, causing power outages and safety risks (Newman et al., 2008). If individuals fledging from nests on man-made structures exhibit NHPI, and adults retain nesting substrate preferences even after significant nest disturbance or destruction, the problems that such nests cause could be perpetuated. If NHPI is indeed a phenomenon common to all monk parakeet populations, this could lead to predictable expansion patterns, particularly at small spatial scales and in urban environments where vegetation types are well known. On the other hand, a degree of flexibility in substrate choice may contribute to their success as an invasive species (Duncan, Blackburn, & Sol, 2003; Wright, Eberhard, Hobson, Avery, & Russello, 2010); such behavioural flexibility has been suggested to be particularly relevant to species capable of both individual and social learning (Wright et al., 2010). For example, for monk parakeets in Argentina, there has been a recent shift to eucalyptus trees *Eucalyptus spp.* (Bucher & Aramburú, 2014) from previously preferred tree species (Volpe & Aramburú, 2011), a shift that has been credited with facilitating large scale range expansion in the species (Bucher & Aramburú, 2014). Likewise, during the invasion of Barcelona, monk parakeets preferred palm trees initially (95%; Sol et al., 1997), but have since shifted to exploiting pines and other substrates. Such flexibility may be indicative of innovation in this species and could influence dispersal capability and resulting dispersal patterns.

In conclusion, our results demonstrate extensive habitat sampling by juvenile monk parakeets and support the hypothesis that a preference for nesting tree type is the result of natal experience in the monk parakeet, at least in one natal habitat type, as opposed to influence from public information regarding the suitability of nesting substrates or vegetation availability. Taking NHPI and breeding dispersal habitat preferences into account could lead to a better understanding of dispersal patterns and improved predictions of range expansion, which is important for the design of effective management strategies for this invasive species.

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4.6 Supplementary material for:

Ranging behaviour and habitat selection in an invasive bird

S1 Correlation between mean and maximum ranging distances

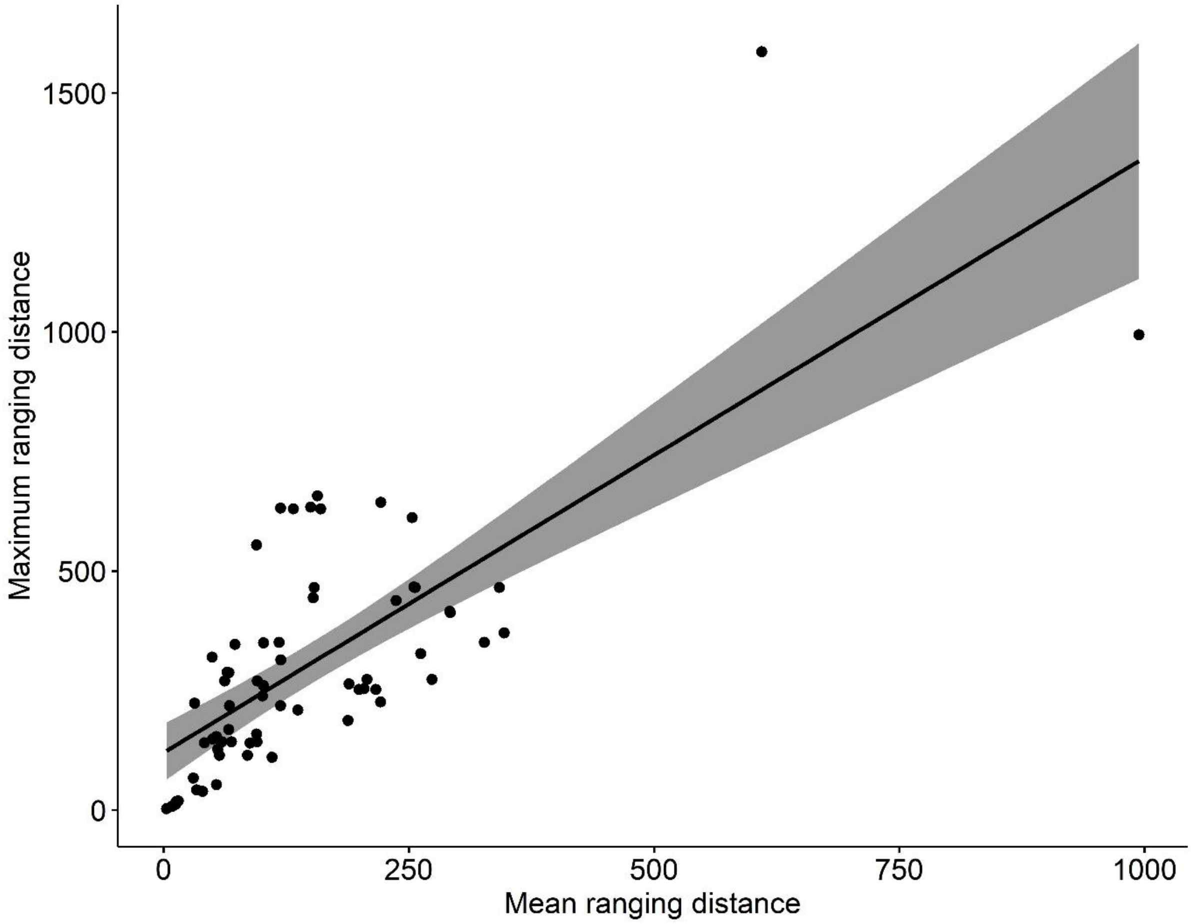

Figure S4.1. Significant positive correlation between mean and maximum ranging distances of juveniles ($r_s = 0.756$, n = 67, $p < 0.001$).

S2. Juvenile ranging distances by sex

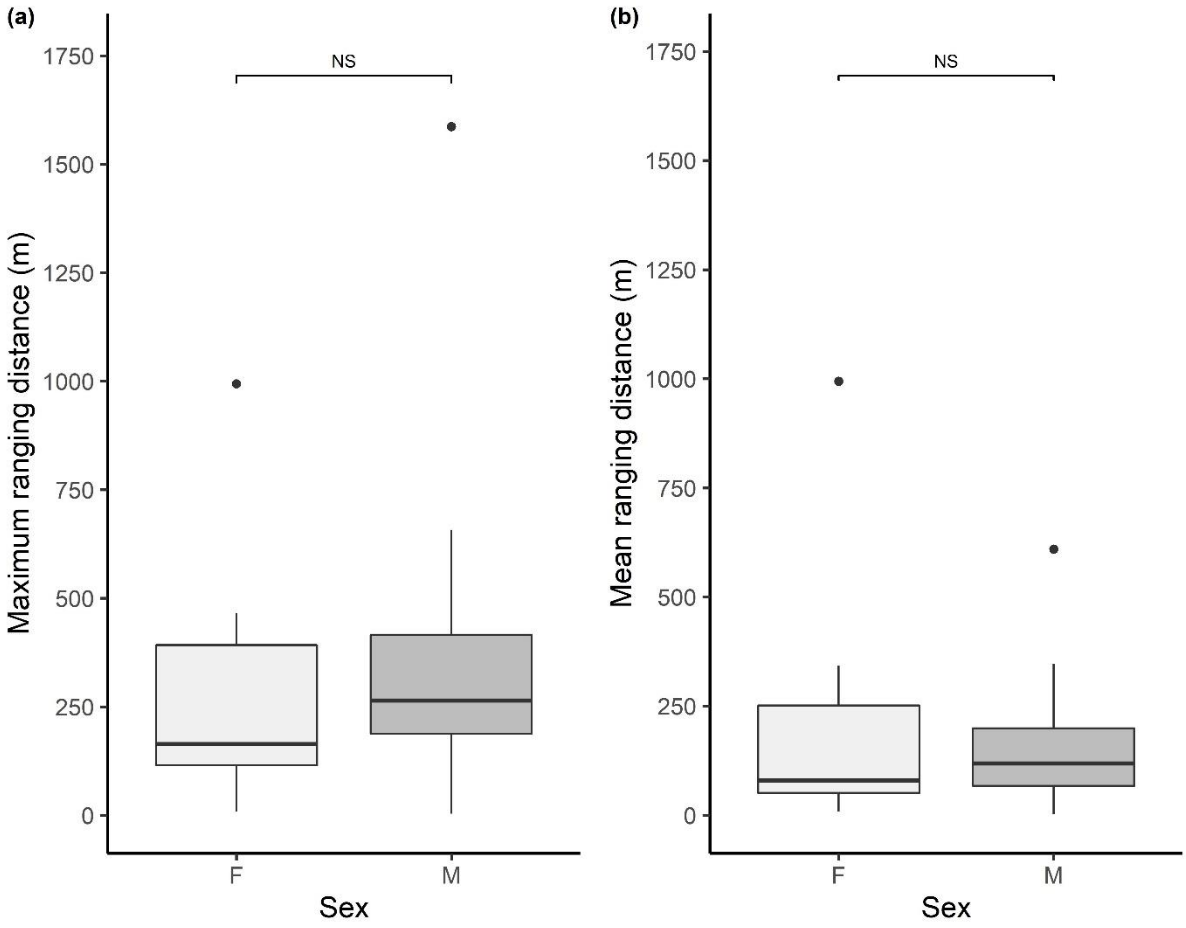

Figure S4.2. a) Maximum and b) mean ranging distances of juvenile birds recorded in the months post-fledging (June-September), males (M; N = 45), and females (F; N = 22). Boxplots indicate the interquartile range (box upper and lower limits), median dispersal distances (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

5. Flexible social organisation and breeding system of a social parrot revealed by genetic analysis

5.1 Abstract

Social organisation and contributions to reproduction vary widely within and between species that breed in groups. Such variation often arises from the process of group formation, which drives patterns of relatedness between group members and results in varying degrees of social conflict and cooperation. Using behavioural observations and molecular genetics, we investigated breeding behaviour in an urban population of the highly social monk parakeet, *Myiopsitta monachus*, to address three objectives. First, we investigated breeding group frequency, composition and formation, finding that about 20% of breeding units were groups, ranging in size from 3-5 birds, the remainder being pairs. Group composition was markedly flexible with multi-male, multi-female and multi-male-female groups observed. Relatedness in breeding groups also varied with some groups containing only non-relatives and others containing a mix of both kin and non-kin. Several routes to group formation were identified, including offspring retention, sibling coalitions and aggregation of unrelated individuals. Secondly, we investigated contributions to building the unusual compound nests of monk parakeets, showing that individuals breeding in groups deliver less nest material than those in pairs, and that males engaged in more nest building and maintenance behaviour than females, including frequent kleptoparasitism of nest material. Finally, we investigated reproductive investment and productivity. Productivity did not differ significantly between breeding attempts made by pairs and groups. We detected extra-pair paternity in 27% of broods raised by social pairs, and shared parentage within some breeding groups, with joint nesting by females detected in multi-female groups, although there were some potentially non-breeding helpers also present. In conclusion, the breeding system of the monk parakeet precludes simple definition, instead showing flexible reproductive roles, with potential for both indirect and direct fitness benefits. More generally, our results add to our understanding of the diversity of parrot breeding behaviour and contribute to our knowledge of breeding systems in social species.

Keywords: breeding behaviour, monk parakeet, *Myiopsitta monachus*, parrot, kleptoparasitism, parentage.

5.2 Introduction

Social organisation and breeding behaviour can vary widely both within and between species that breed in groups. For instance, breeding attempts may involve: a breeding pair with non-breeding 'helpers', aggregations of largely monogamous co-breeding pairs, or various systems of cooperative polygamy in which more than one male or female, or both participates in breeding within a group (Cockburn, 1998; Clutton-Brock, 2016; Koenig & Dickinson, 2016; Rubenstein & Abbot, 2017). Among vertebrates, breeding in groups is obligate in a few species where breeding without additional help is rare or unsuccessful (e.g. Heinsohn, 1992), while in most species, breeding in a group is facultative and can be successful without additional assistance (e.g. Hatchwell, 1999). Whether systems involve co-breeding or 'helping', cooperative breeding strategies result in more than two individuals engaging in parent-like behaviour to raise young from a single brood or nest (Emlen, 1991; Hatchwell & Komdeur, 2000). Such parental behaviour is varied and can include: territory maintenance activities and defence (Taborsky, 1984; Josi, Taborsky, & Frommen, 2020), babysitting young (Clutton-Brock et al., 1998), and allofeeding incubating individuals and feeding young (Lloyd, Taylor, Du Plessis, & Martin, 2009).

There are multiple routes to group formation, for example individuals within a group may be: offspring that have delayed dispersal (Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992), failed breeders (MacColl & Hatchwell, 2002) or immigrants to the territory (Seddon et al., 2005). Group composition can therefore be markedly diverse and include juveniles, adults or a mixture of both (Preston et al., 2013; Barve et al., 2021), and groups may be composed of relatives, unrelated individuals, or a mixture of kin and non-kin (reviewed in Hatchwell, 2009; Riehl, 2013) and additional group members may be either almost exclusively male (Hatchwell, Russell, Fowlie, & Ross, 1999), majority female (Komdeur, 1996) or a mixture of both sexes (Preston et al., 2013).

There are various avenues for conflict to arise within groups, for instance cooperative group members may experience interference competition when foraging together, with dominants excluding subordinates from the richest foraging areas (Radford & Du Plessis, 2003). In cooperative breeding systems with helpers, conflict can also arise around the amount of effort or investment subordinate group members make, for example, individuals may be ‘punished’ for not providing assistance in a ‘pay-to-stay’ system (Fischer, Zöttl, Groenewoud, & Taborsky, 2014). There can also be reproductive conflict within groups, for instance over access to breeding opportunities which may be limited to just a pair of individuals within the group, and can be enforced by aggression (Hannon, Mumme, Koenig, & Pitelka, 1985; Kutsukake & Clutton-Brock, 2006) and stress-related reproductive suppression (Young et al., 2006). There can also be significant reproductive conflict over sharing a breeding attempt with other individuals when co-breeding; limits to litter or clutch size may reduce per capita offspring numbers for co-breeding individuals (Koenig, 1981). This conflict can lead to egg destruction (Koenig, Mumme, Stanback, & Pitelka, 1995) or the killing of offspring (Kutsukake & Clutton-Brock, 2006) by other group members.

Breeding in groups can also bring a variety of fitness benefits for breeders, co-breeders and helpers. For those species in which breeding in groups is obligate, breeding together enables successful reproduction (Heinsohn, 1992). There is evidence that additional group members can increase juvenile survival (McGowan et al., 2003), nestling or fledgling condition and body mass (te Marvelde, McDonald, Kazem, & Wright, 2009; Bolopo, Lowney, & Thomson, 2019), the overall probability of successful reproduction (Josi et al., 2020), and may help to delay senescence in the breeding members of the group (Hammers et al., 2019). There are also direct benefits additional groups members or helpers can accrue including: access to breeding opportunities within their group (Emlen, 1996; Richardson, Burke, & Komdeur, 2002), further reproductive opportunities beyond the group via extra-pair copulations (Mulder, Dunn, Cockburn, Lazenby-Cohen, & Howell, 1994) and lower risk of mortality due to protection by other group members or shelter in the shared territory (Taborsky, 1984; Taborsky, 1985).

Kin selection, that is selection for traits due to their beneficial effects on the fitness of relatives, is vital in our understanding of the inclusive fitness benefits derived from helping to raise related offspring (Hamilton, 1964). Kin may cooperate in a number of ways, for example in raising young (e.g. Preston et al., 2013) and by individuals directing their investment in public goods towards kin (e.g. van Dijk et al., 2014). The kin-selected benefits of helping or co-breeding with relatives are derived from an increase in the production of non-descendant kin, resulting in an increase in an indirect component of an individual's inclusive fitness (reviewed in Cockburn, 1998; Dickinson & Hatchwell, 2004). Such benefits may be key drivers in the formation of breeding groups.

The monk parakeet, *Myiopsitta monachus*, is a medium-sized parrot (weight 127-140 g) native to South America, with invasive populations found almost worldwide (Forshaw, 1989; Russello, Avery, & Wright, 2008; Bush, Baker, & Macdonald, 2014). Unusually amongst parrots, monk parakeets are not cavity nesters; instead individuals use interlaced sticks to construct large, conspicuous nest structures that can contain a single nest chamber or multiple individual nest chambers in a compound structure (Forshaw, 1989; Eberhard, 1998; Spreyer & Bucher, 1998). The nests can vary widely in size and number of occupants; single nest structures have been reported to contain up to 100 pairs of parakeets (Naumberg, 1930), and have been recorded with 60 individual chambers (Burger & Gochfeld, 2005). However, where the species is heavily managed, such as in urban areas, the number of chambers per nest is typically lower, for instance in Catalonia the majority of nests contain only one or two chambers, although nests with up to 36 chambers have been reported (Domènech et al., 2003). Nest structures are frequently aggregated, with large groups of nests occupying the same or neighbouring trees (Bucher, Martin, Martella, & Navarro, 1991; Eberhard, 1998). Previous studies have revealed that relatives are clustered within these compound nests and within shared nesting trees, resulting in 'kin-neighbourhoods' that form through limited and coordinated natal dispersal and high breeding site fidelity (Dawson Pell et al., 2021).

Reports of cooperative breeding in the parrot family are scarce with just 5% of parrots described as cooperative (Cockburn, 2006). Monk parakeets have been reported to display several characteristics indicative of cooperative breeding, for instance, reduced dispersal and delayed breeding (Bucher et al., 1991). In addition, there is some limited evidence of possible helpers assisting breeding attempts (e.g. Bucher et al., 1991; Bucher, Martínez, & de Aranzamendi, 2016), with 'helpers' observed aiding adults to feed young (Eberhard, 1998). In addition, genetic evidence from a single breeding trio in South America points towards a high degree of relatedness in groups; the male 'helper' was a full sibling of the breeding male (Bucher et al., 2016). However, this limited evidence is anecdotal and questions still remain about the breeding system of the monk parakeet, including questions regarding the frequency of breeding in groups, the composition of breeding groups in terms of sex, age and relatedness between cooperating individuals, and whether groups consist of a breeding pair with helpers, joint-nesting monogamous pairs, or groups of co-breeding individuals in a system of cooperative polygamy. A combination of molecular genetic investigations and detailed field observations is required to address these research questions.

In this study, we conducted an investigation into the breeding behaviour of an urban population of monk parakeets. We addressed three main aims: first, we characterised breeding behaviour by quantifying the frequency of nest chambers being attended by breeding pairs and groups, and examining group characteristics and composition. We also explored the routes to group formation and genetic relatedness within breeding groups and between breeding pairs. Second, we examined nest-building behaviour by both pairs and groups and investigated cooperation and conflict over contributions to nest building. Finally, we examined reproductive parameters in pairs and groups and undertook a parentage analysis to examine evidence of extra pair paternity and co-breeding in our study population.

5.3 Materials and methods

5.3.1 Study site and species

We monitored the behaviour of monk parakeets at nests in Ciutadella Park, Barcelona, Spain (41.39°N 2.17°E) on the north-east coast of the Iberian Peninsula. Ciutadella Park comprises approximately 30 ha of native and exotic vegetation and contains a high density of monk parakeet nests.

In order to be able to make observations on individually identifiable birds, monk parakeets in our study population are marked using both aluminium leg rings and highly visible, unique neck collars that allow for individual identification up to 40 m distance (Senar et al., 2012). To capture birds for ringing, we used either gas-propelled nets, a baited trap controlled remotely, caught birds in the nest during incubation, or ringed them as nestlings. It is estimated that approximately 64% of the breeding population was individually marked during the period of data collection for this study. We used a cherry picker to access nests; no birds abandoned their nests as a result of disturbance caused by these nest visits. We could only accurately record the age of birds that were marked as nestlings (individuals caught in their first breeding season are not distinguishable by eye from adults), we could however assign birds a minimum age based on the date they were ringed if they were caught as adults.

5.3.1.1 Compliance with ethical standards

JCS received special authorization (001501-0402.2009) for the handling of animals in research from Servei de Protecció de la Fauna, Flora i Animal de Companyia, according to Decree 214/1997 /30.07. Birds were handled and blood samples taken with special permission EPI 7/2015 (01529/ 1498/2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan regional ethical guidelines for the handling of birds.

5.3.1.2 DNA extraction and genotyping

For genetic analyses and sex determination, blood samples (maximum 100 µl) were extracted from the brachial or jugular vein of each individual during ringing. For details of blood sample storage and DNA extraction technique see Dawson Pell et al. (2020). As male and female monk parakeets are not distinguishable in the field, marked birds were sexed using the sexing marker, Z002B (Dawson, 2007). Initially, individuals were genotyped at 26 microsatellite loci optimised in 6 multiplexes, however, following assessments of marker quality we used 21 of these loci in analyses. These markers were: Mmon01, Mmon02, Mmon03, Mmon04, Mmon07, Mmon09, Mmon10, Mmon11, Mmon13, Mmon14, Mmon15, Mmon16 (Dawson Pell et al., 2020), MmGT060, MmGT046, MmGT105, MmGT030, MmGT071, MmGT057 (Russello, Saranathan, Buhrman-Deever, Eberhard, & Caccone, 2007), TG03-002 and TG05-046 (Dawson et al., 2010), and CAM-20 (Dawson et al., 2013). For further details of multiplexes and marker quality assessment see Dawson Pell et al. (2021). PCR (polymerase chain reaction) and allele scoring protocols were identical to those followed in Dawson Pell et al. (2020) and all alleles were scored blind to the identity and sex of the bird.

5.3.1.3 Behavioural observations at the nest

Behavioural observations were conducted during the breeding season from April - July 2018 and 2019 at nests in ten large, mature pine trees, *Pinus halepensis*, in Ciutadella Park. Prior to commencing nest observations, we surveyed trees for the presence of nests and individually labelled each nest chamber with a removable, numbered tag visible from the ground. No individuals deserted their nest due to disturbance caused by nest labelling. Ciutadella Park is a public access park and monk parakeets are habituated to regular human presence in close proximity to their nests.

Each nest was observed for one hour every two - seven days in 2018 and one hour every two - eleven days in 2019 depending on weather conditions and park maintenance activities. Multiple nests were observed simultaneously in a single nesting tree by the observer (FSEDP) from the ground using binoculars. Observation periods of each nest alternated between the morning and afternoon. Observation session times were also alternated within both the morning and afternoon to cover the range of available daylight hours. A total of 390 observation hours were conducted across two years (2018: total 263 h, 22 h per chamber; 2019: total 127 h, 14-15 h per chamber).

In the 10 focal pine trees there were 72 nests containing 149 individual nest chambers at the end of the observation period in 2018, 112 of the chambers were occupied and 74 were actively used in breeding attempts. These nests were occupied by 113 marked individuals and at least 64 unmarked individuals during this observation period. In 2019, there were 81 nests containing 98 chambers, 92 of which were occupied and of these, 76 were used in breeding attempts. There were fewer unoccupied chambers in 2019 due to maintenance activities in the park which removed all the monk parakeet nests in pine trees in July 2018, so there were no older, more established nests in 2019. Nests in 2019 were occupied by 103 marked individuals and at least 64 unmarked individuals. The age of observed birds ranged from one year old to at least 13 years old based on ringing data.

5.3.2 Breeding group composition and formation

Using data collected during nest observations, we characterised breeding behaviour in the monk parakeet as follows. We determined the number of individuals attending a nest chamber to identify pairs and groups engaged in breeding attempts. In addition, we recorded group sex composition, the age of group members and the genetic relatedness between members of breeding groups. To estimate the minimum age of birds that were not ringed as nestlings, we used the date they were caught and ringed as adults as an indicator of their minimum age. We assessed the persistence of breeding groups by comparing group membership across years.

To estimate pairwise genetic relatedness between individuals in breeding pairs and groups relatedness was calculated in SPAGeDi version 1.5 (Hardy & Vekemans, 2002) using Queller and Goodnight’s (1989) coefficient of relatedness. We used the genotypes of all adult individuals nesting in the 10 focal trees in 2018 and 2019 (N = 134) to generate the allele frequencies for estimating genetic relatedness. For breeding pairs of birds in which both individuals were marked and genotyped we examined dyadic relatedness within social pairs and compared mean relatedness of all pairs to zero using a t-test. For breeding groups, we extracted relatedness values for dyads of individuals and also calculated mean relatedness values for each group. We compared pairwise relatedness between same-sex and opposite-sex group members using t-tests. We removed dyads that were present in both years from the dataset, so each dyad was included only once.

In addition, we used the social pedigree of birds from our study site to explore routes to breeding group formation in this species. Our limited social pedigree began in 2017 with a large ringing effort for offspring fledging in that year. Nestlings were also ringed in 2018 and 2019 and combined with extensive nest observations we were able to assign social parents to these birds. The social pedigree could be relevant to individuals as this may be the information individuals readily have access to if kin recognition relies on learned associations.

5.3.3 Nest-building behaviour

During nest observation periods we recorded: the identity of nest occupants (if marked), all incidents of nest-building and maintenance behaviours, theft of nesting material, nest defence, observable social interactions (i.e. preening, copulating, allofeeding) and nest chamber visits (see *Investment by group members*). We considered the delivery of nesting material, for example, sticks or palm leaves, to be incidents of nest-building behaviour and we defined nest maintenance behaviours as when a stick or nest lining material was manipulated or moved around the nest structure as opposed to the delivery of new material collected away from the nest. In 2018, one nest was partially obscured from observation from the ground. Sticks delivered to this nest could be recorded but nest maintenance activities could not, so the two birds occupying this nest were excluded from analyses of maintenance behaviour. For all other nests building and maintenance behaviours were recorded in both years. Nest material kleptoparasitism was recorded when we observed nesting material taken from one nest and delivered to another. Nest defence was defined as any occasion an individual attempted to displace a bird that was attempting to steal nesting material from their nest, including vocalisations and/or chases. Monk parakeets are sexually monomorphic in the field (Forshaw, 1989), so behavioural observations were made blind to the sex of birds, genetic sex-typing being used after the field season to determine sex.

To investigate if the sex of an individual or whether an individual is breeding in a pair or group influences their nest building behaviour, we initially conducted a negative binomial GLMM on the number of building events, including ID as a random factor, and sex, breeding group (yes/no), the interaction between sex and whether individuals are part of a breeding group or not, and year as fixed effects. However, only around half of the birds were observed in both observation years, so the random effect prevented model convergence. Therefore, we applied a negative binomial GLM including the data for all individuals, that included sex, breeding group (yes/no), the interaction between sex and whether individuals were part of a breeding group or pair, and year as explanatory factors. We then ran a second analysis on a more conservative dataset that included data for birds that were observed in only one year, to rule out the possibility that any results in the first analysis were driven by repeated observations on certain individuals. We repeated the same two analyses on the number of maintenance events. We achieved model simplification through stepwise backwards elimination (Crawley, 2005); we compared models using likelihood ratio tests and terms were removed by order of least significance. Significance values for retained terms were obtained by comparing the minimal model with a model from which we removed the term of interest. P values for dropped terms were calculated by comparisons between the minimal model without the term included and a model including the term. For breeding groups, we also examined the building and maintenance efforts of group members to determine whether they differed in their investment in the shared nest.

We ran similar models examining the number of theft events observed including sex and year as explanatory factors. Due to low sample sizes, we ran just one model on nest defence events that included all individuals and sex and year as explanatory factors. One nest defence event by a non-resident was excluded. We also investigated whether multiple group members engaged in nest defence. All statistical analyses were performed in R version 3.5.0 (R Core Team, 2018).

5.3.4 Productivity and reproductive investment

5.3.4.1 Productivity of pairs and breeding groups

We compared clutch sizes produced by pairs and breeding groups using a poisson GLM, with year as an additional explanatory factor. The number of chicks attaining ringing age (a proxy for fledgling number; the last of the 2-3 nest visits per breeding attempt was timed to coincide with chicks reaching ringing age) was also compared for pairs and breeding groups. We examined whether breeding groups or pairs were more likely to fledge offspring at all using a binary logistic regression generalised linear model (GLM) with a logit-link function, including year as an explanatory factor. Then, using only pairs and groups that fledged at least one chick, we compared the number of chicks attaining ringing age using a poisson GLM, again including year as an explanatory factor. We also compared clutch sizes for multi-female breeding groups and multi-male breeding groups using a Wilcoxon rank sum test. Fieldwork constraints meant that we collected data from first-broods only.

5.3.4.2 Investment by group members

We investigated provisioning of offspring using two sets of data. First, we observed nest visits in dedicated nest observation periods during the nestling phase. Nest visits were recorded when an individual entered a nest chamber; to be conservative and avoid ambiguity, we only recorded a nest visit when a bird was not overtly entering a nest chamber to engage in nest-building or maintenance activities, i.e. carrying nesting material or entering the chamber only to manipulate material around the entrance. Nestling provisioning in the monk parakeet cannot be observed directly because feeding is by regurgitation within the nest chamber, so we assumed any bird entering the nest chamber had the possibility of provisioning nestlings. Notably, nest visits could occur for a variety of reasons, including incubating or feeding offspring, or for rest, although the reason could often not be determined by the observer unless mature nestlings were visible in the nest entrance. Secondly, we recorded instances of fledglings being fed by identifiable adults outside the nest. These feeding events occurred either in the natal tree during nest observation periods or during surveys of the field site. These surveys were conducted for a concurrent study into dispersal behaviour in the monk parakeet and totalled over 380 hrs and covered areas up to 6 km from Ciutadella Park; for full details see Dawson Pell et al. (2021). We identified instances of young from breeding groups being fed outside the nest to assess whether provisioning was conducted by multiple group members. We also recorded any incidents of offspring begging to members of breeding groups, which may be indicative of provisioning by multiple group members.

5.3.4.3 Copulations and parentage patterns

To determine the mating patterns of monk parakeets we recorded all copulations seen during nest observation periods and during surveys of the field site, noting in particular whether any observed matings were outside the social pair or group.

We determined parentage of 27 broods (17 in 2017 and 10 in 2018) in Ciutadella Park, including Passeig de Lluís Companys and Plaça de Tetuan. In 2018, social parents were identified during dedicated nest observations totalling 263 hours; in 2017, nest occupants were identified in surveys of Ciutadella Park and surrounding areas, with 73 trees observed for approximately 2 hours each (total of c. 146 hours). Therefore, we are confident that social parents were correctly assigned in 2018, but the more limited observations in 2017 led us to assess parentage more cautiously in that year. We included in these analyses only those broods that had all social parents marked and genotyped and all marked chicks genotyped too.

Blood samples were collected when nestlings were ringed and marked with a medal, so genotypes were obtained only for nestlings that reached > 21 days old; DNA samples were not collected from unhatched eggs, nor from nestlings that died before 21 days old. Therefore, parentage data is incomplete, but our results do shed light on the patterns of parentage in this species.

We performed parentage analyses using the maximum likelihood approach applied in Cervus version 3.0.7 (Kalinowski et al., 2007). To estimate allele frequencies for the analysis we used all parents and offspring from 2017 and 2018 included in analyses (N = 249) initially with the 21 loci detailed in *DNA extraction and genotyping*. During initial trials of the parentage analyses we noted that a large proportion of observed mismatches between offspring and their social mother occurred at one locus

(Mmon07). Further examination showed that all such mismatches at this locus were caused by a single base-pair difference, and so were more likely to be caused by scoring error rather than real differences between alleles. Consequently, we removed this locus from the genotype file before conducting the parentage analysis.

We performed separate parentage simulations and analyses for broods attended by social pairs and by breeding groups, and parentage simulations were run independently for 2017 and 2018 due to the different numbers of marked candidate parents in each year and to prevent individuals being included in both the offspring and parent databases. For broods attended by social pairs we assigned the social mother as the known parent and then ran paternity simulations and analyses. For individuals from nest chambers attended by groups we conducted parent pair simulations and analyses, as we could not be certain of the identity of the putative mother of the chicks, particularly when more than one female was present at the nest. In each year we included all genotyped adults as potential parents; in 2018 we included 66 possible candidate fathers (in pair and group analyses) and 46 possible candidate mothers (in the parent pair analyses only), and in 2017 we included 42 possible fathers (in both analyses) and 29 possible mothers (parent pair analyses only). We also took account of relatives in the population during the simulations; previous investigations revealed that relatives of both sexes live in close proximity in shared compound nests and/or nesting trees (Dawson Pell et al., 2021), which may influence the results of a parentage analysis. To assess the number of relatives within the pool of candidate mothers and candidate fathers we used maximum likelihood relationship estimations in ML-RELATE (Kalinowski et al., 2006), and quantified the proportion of individuals assigned as either parent-offspring relationships or full-sibling relationships in 2018. For females, this estimate was 3% between candidate mothers and for males it was 2% between candidate fathers. These estimates were included in simulations of parentage in both years. To estimate the proportion of sampled candidate parents we used the numbers of marked and unmarked birds within the 10 focal trees in 2018 because these numbers were the result of the most extensive observations. In 2018 there were 113 marked and 64 unmarked birds in the 10 trees, therefore we estimated that approximately 64% of the population was sampled and used this as the proportion of potential parents that were sampled for both years. Both simulations used 100,000 offspring, estimated genotype error rate of 3.1% (based on previous estimates; see Dawson Pell et al., 2021), 64% of candidate parents sampled, a minimum of 10 loci typed, 2% male relatives (both analyses) and 3% female relatives (parent pair simulation only) and 97% loci successfully typed (calculated during allele frequency analysis). We examined all mismatches with assigned parents thoroughly and accepted those with one mismatch between offspring and likely parent. One offspring in the paternity analysis had two mismatches with both the likely mother and father, however as these were the social parents and the trio (offspring, mother and father) was assigned with 95% confidence we accepted this assignment.

5.3.4.4 Relatedness within broods

To corroborate results of parentage analyses we also used SPAGeDI (Hardy & Vekemans, 2002) to estimate pairwise relatedness within broods using Queller and Goodnight's (1989) coefficient of relatedness. We compared pairwise relatedness within broods that showed evidence of having sexually monogamous parents to relatedness values from within broods that showed evidence of either extra-pair paternity or mixed parentage (e.g. co-breeding), using a linear mixed model, with EPP/mixed parentage (Y/N) as a fixed effect and brood ID as a random effect. We also compared mean relatedness for broods with evidence of EPP/mixed parentage and those with no evidence using a Wilcoxon rank sum test. Maximum likelihood estimates of relationships between social siblings in ML-RELATE (Kalinowski et al., 2006) were also used to assign relationships as full-sibling, half-sibling and unrelated individuals. Finally, we visually assessed the relationship estimates from ML-RELATE against the relatedness estimates from SPAGeDI to see whether similar patterns arose using these different approaches.

5.4 Results

5.4.1 Breeding group composition and formation

5.4.1.1 Breeding group composition

Most nest chambers used for breeding were occupied by a breeding pair, but some were occupied by groups of 3-5 individuals (Figure 5.1). Of 74 nest chambers that had active breeding attempts in 2018, 61 (82%) contained a breeding pair and 13 (18%) contained a breeding group. Three of these breeding groups also occupied a second nest chamber that was not used for breeding. A further two chambers were occupied by non-breeding groups, one containing three birds and the other four. Similarly, of the 76 nest chambers used in breeding attempts in 2019, 61 (80%) contained breeding pairs and 15 (20%) contained groups of three or more birds (Figure 5.1). One group bred simultaneously in two different nest chambers. Three further nests occupied by groups of three or more birds were identified but one was inaccessible via cherry picker so any breeding attempts could not be recorded and the other two were alternative roosting chambers for groups breeding in another nest chamber.

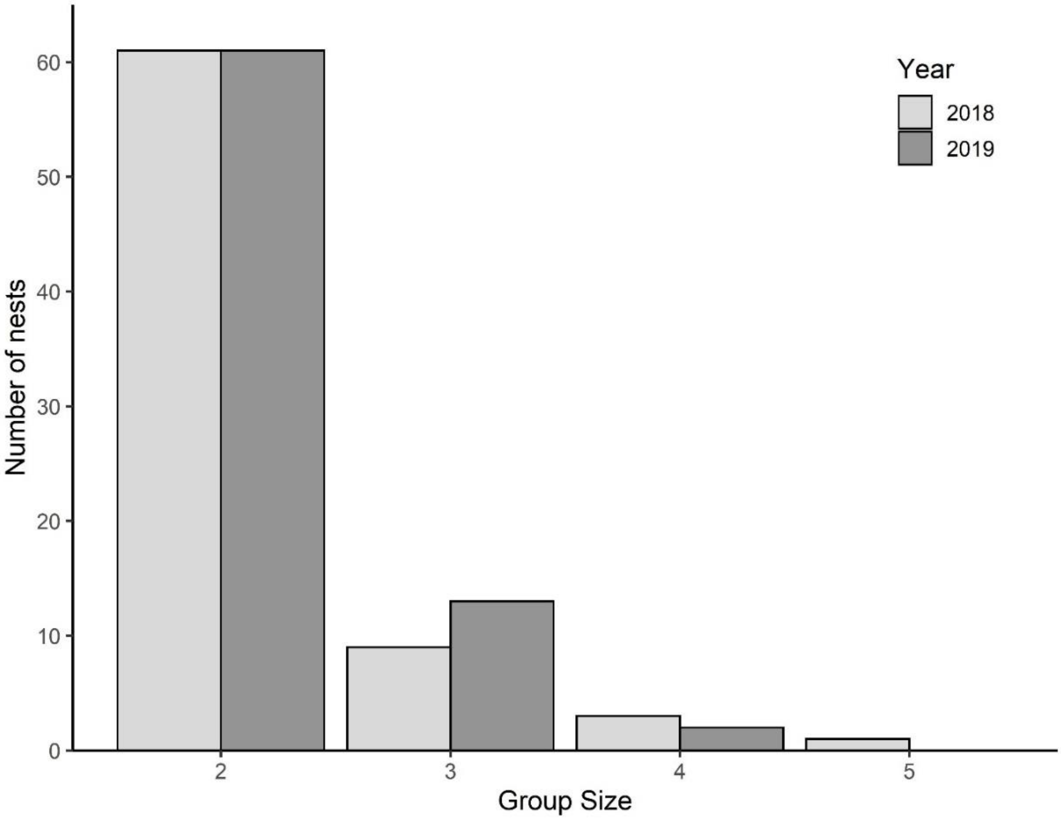

Figure 5.1. Number of nest chambers attended by pairs (group size = 2) and breeding groups (group size 3-5) in 2018 (N = 74 nest chambers) and 2019 (N = 76 nest chambers).

These are potentially conservative estimates of the frequency of breeding groups in our study population. In cases where some or all of the birds attending a nest were unmarked, unless they were all observed together we would not necessarily identify that there was a group. However, our intensive observations at nests suggest that such cases were minimal.

Across both years, the mean size of groups (i.e. excluding pairs) engaged in breeding attempts was 3.3 ± 0.5 SD (N = 27). We ringed all birds in 13 out of 27 groups; the other 14 groups contained at least one unmarked individual. Genetic sex-typing revealed flexibility in group composition; in both years we identified groups that contained: one female and more than one male (i.e. 'multi-male' groups), one male and more than one female ('multi-female' groups), and one group in each year that contained two or more of both sexes ('multi-male-female' groups; Figure 5.2). Sex was deduced for six unmarked birds (two in 2018 and four in 2019), as these groups all contained two or three marked males and a single unmarked bird, in each of these cases a breeding attempt was made therefore the unmarked bird in each case was assumed to be female. Overall, group composition across two years was: multi-male 46%, multi-female 15%, multi-male-female 8% and unknown 31%. All groups of unknown sex composition could only have been multi-male or multi-female as they consisted of three birds each.

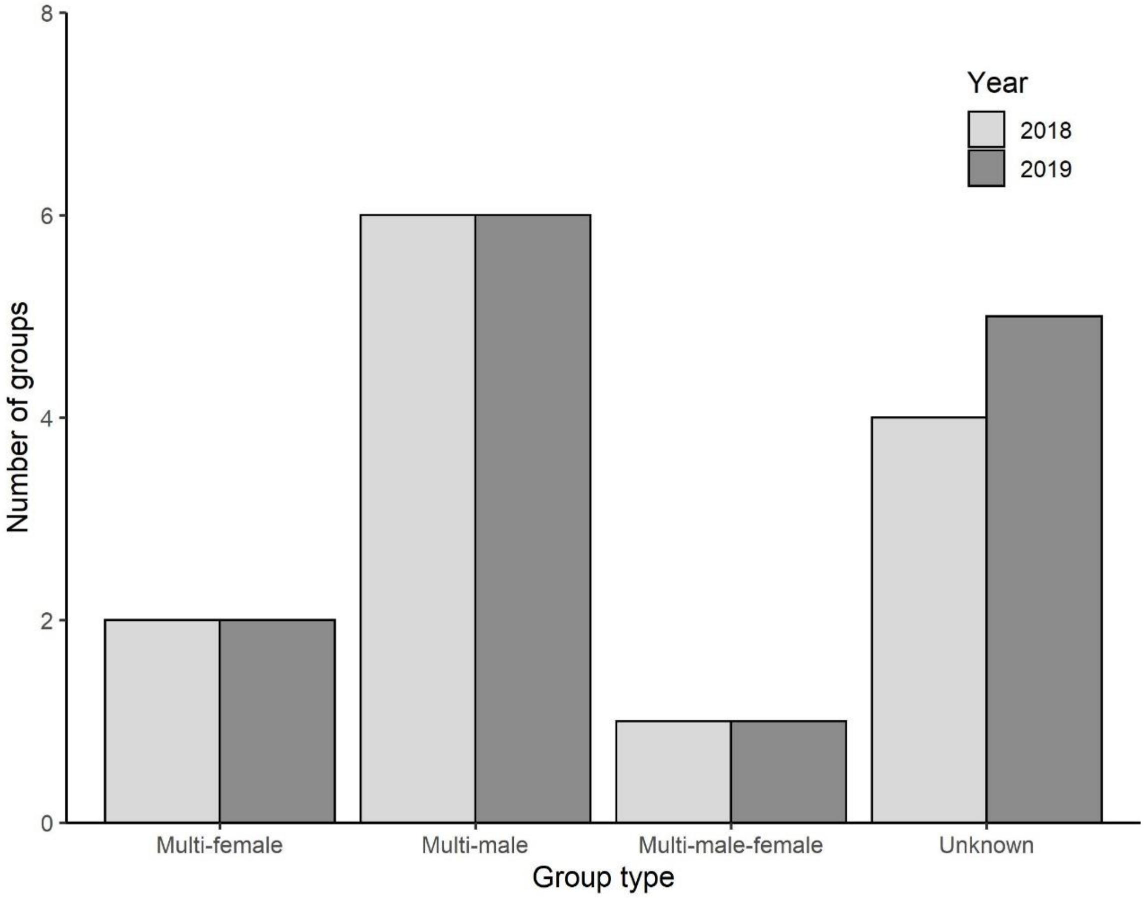

Figure 5.2. The number of each group type; multi-female, multi-male and multi-male-female in 2018 and 2019. N = 27 groups. Groups shown here engaged in breeding attempts, groups not engaged in breeding are not included.

5.4.1.2 Breeding group formation

Social pedigree - Based on the limited social pedigree, we identified several avenues for group formation in the monk parakeet. Eight (31%) out of the 26 breeding groups contained one-year-old birds nesting together, seven of which were (social) siblings that fledged from the same nest chambers the previous year; the other group contained three one-year-old birds all from different nest chambers. The seven groups containing (social) siblings consisted of six male duos and one male trio of siblings breeding with another individual. We also detected four groups (15%) where offspring (three females, two males) remained with either one or both parents to form a group. The social pedigree was insufficiently complete to identify the route to group formation for the remaining groups in this study.

Genetic pedigree – Fourteen out of the 27 groups contained at least one unsampled individual, so not all genetic relationships between individuals within groups could be assessed. Pairwise relatedness values between group members varied markedly, ranging from unrelated individuals to relatedness expected for 1st order kin (range -0.41 to 0.67; mean group relatedness range from -0.29 to 0.67 when all groups included; Figure 5.3a, b) and similar patterns were observed for groups with all members marked (Figure 5.3c, d). These results indicate that some groups contained multiple close relatives and others contained no related individuals and further suggests that routes to group formation in the monk parakeet are flexible. High relatedness between at least some group members is to be expected based on the data from our social pedigree, and we have confirmed that pattern here using genetic data.

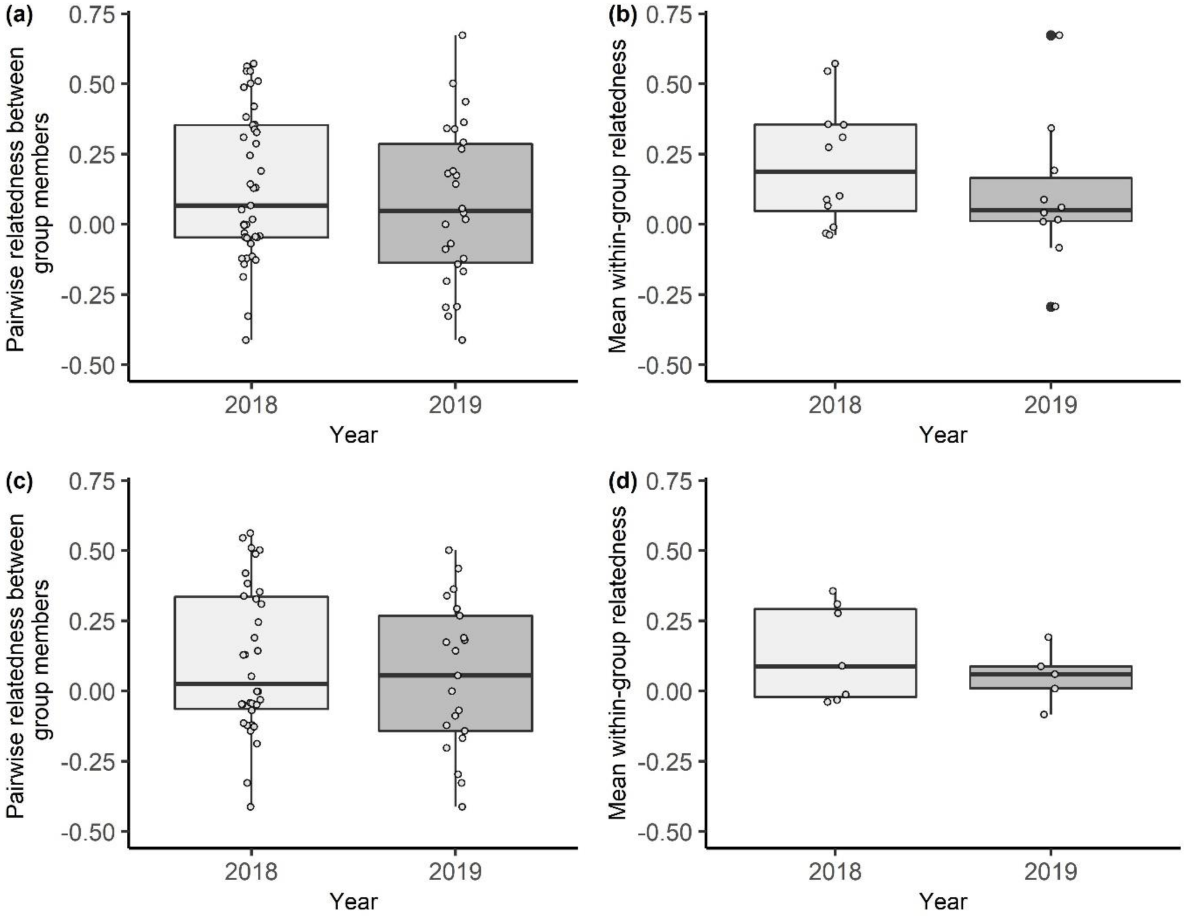

Figure 5.3. a) Pairwise relatedness between members of breeding groups 2018 (N = 41 pairwise comparisons) and 2019 (N = 26 pairwise comparisons) including all individuals and b) mean group relatedness values for breeding groups 2018 (N = 12 groups) and 2019 (N = 10 groups) when all

groups with at least one comparison were included. c) Pairwise relatedness between breeding group members 2018 (N = 34 pairwise comparisons) and 2019 (N = 21 pairwise comparisons) only including birds for which the whole group was genotyped and d) mean within-group relatedness values for breeding groups in 2018 (N = 7 groups) and 2019 (N = 5 groups) only including groups in which all birds were genotyped. Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots)

A substantial number of pairwise comparisons within breeding groups would involve mates, which are unlikely to be related (see *Relatedness within breeding pairs*). To investigate whether same-sex birds were more related than opposite-sex birds within groups, we compared pairwise relatedness between same-sex and opposite-sex dyads. As expected, same-sex relatedness was significantly higher than opposite-sex relatedness when we included dyads from all groups, some of which had unmarked birds (t = -2.259, p = 0.028; Figure 5.4), and approached statistical significance when we included only dyads from groups with all birds marked and genotyped (t = -1.998, p = 0.053; Figure 5.4).

We also sought to confirm the genetic relationship between individuals in breeding groups that we had ringed in the nest and assigned as social siblings. Relatedness between social siblings ranged from -0.003 to 0.673, with mean relatedness of 0.293 ± 0.239 (N = 8 dyads; Figure S5.1), indicating that social siblings may actually include full-sibs, half sibs and possibly unrelated individuals (see *Copulations and parentage patterns* for further data).

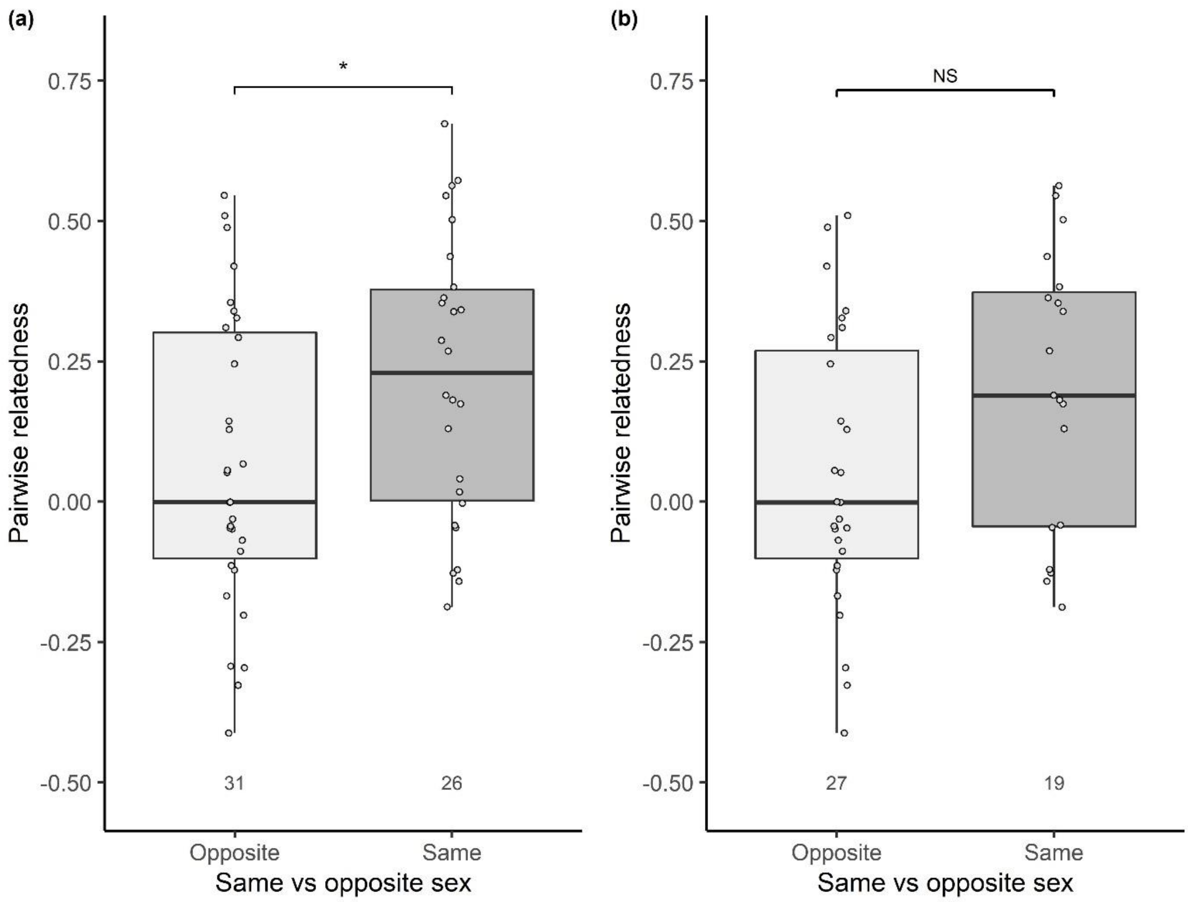

Figure 5.4. Pairwise relatedness for dyads from breeding groups comparing opposite-sex and same-sex dyads for a) all breeding groups including with some unmarked birds and b) breeding groups containing all marked birds only. Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots). Sample sizes are given above the x-axis. *$p < 0.05$.

5.4.1.3 Relatedness within breeding pairs

We examined relatedness between pair members in 2018 (N = 18 pairs) and 2019 (N = 9 pairs; note that six pairs present in 2018 and 2019 were included just once). Mean relatedness within pairs (-0.02 ± 0.17 SD, range: -0.34 to 0.33,) was not significantly different from 0 (t = -0.481, p = 0.634, N = 27; Figure 5.5), indicating overall relatedness between pairs was low as would be expected in a population with no significant inbreeding detected (Dawson Pell et al., 2021). However, there were a few pairs where relatedness levels approximated that expected for 2nd order kin.

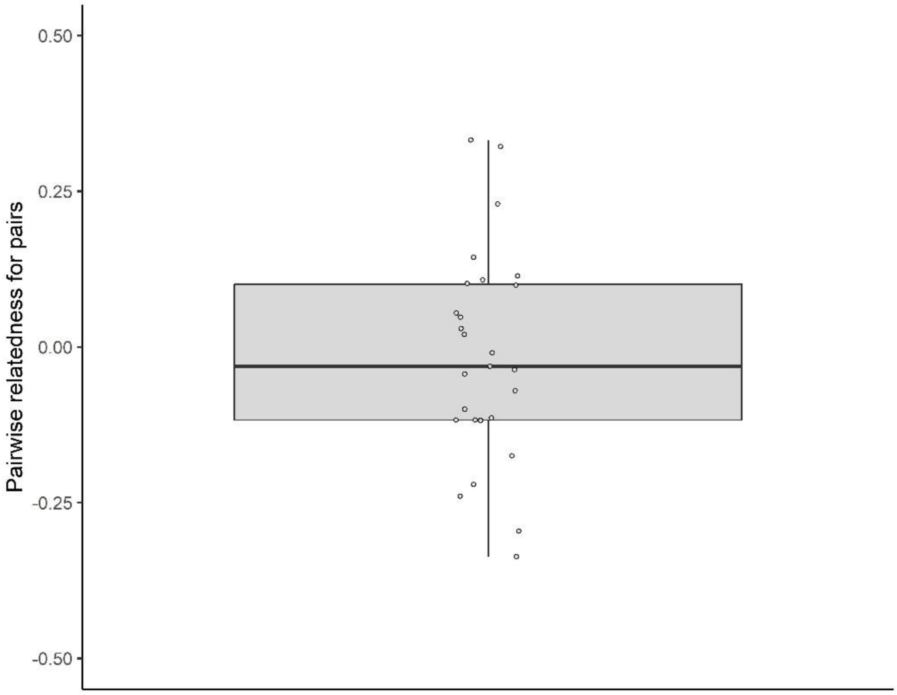

Figure 5.5. Pairwise relatedness values between monk parakeet breeding pairs (N = 27 pairs). Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots)

5.4.1.4 Persistence of group associations

One entire breeding group from 2018 nested together in 2019, and two others groups lost just a single group member between years. In both these latter cases the missing bird was not observed elsewhere in the study site and may have dispersed or died. No members from three groups present in 2018 were observed at the study site in 2019. For all other groups, at least one group member was observed at the study site, either paired with a previous group member having lost the other group members, or paired with another bird not from the original group. This limited evidence indicates that while some group associations are stable over multiple breeding seasons, the majority are not. It should be noted that at the end of the 2018 breeding season all nests in Ciutadella Park were removed during park maintenance, potentially disrupting monk parakeet groups.

5.4.1.5 Age of breeding group members

Some breeding group members were marked as nestlings (N = 31) so their precise age was known, while birds trapped as adults had a minimum age assigned (N = 37). The age of breeding group members ranged from one-year-olds to at least six years old (mean 2.1 ± 1.6 including birds with minimum ages assigned, mean 2.2 ± 1.6 SD when repeat birds were only included at their older age). Within group ages varied as expected given our results for the routes to group formation; some groups contained a mixture of young (first breeding season) and older birds up to six years old, other groups contained only young birds (first breeding season), and some groups contained only older individuals; for example, one group contained three birds all at least six years old. This indicates that group formation is not just the result of young birds joining more experienced individuals in breeding groups, but groups can also involve aggregations of older individuals or inexperienced birds.

5.4.2 Nest-building behaviour

5.4.2.1 Nest building and maintenance

Between April and July 2018 and 2019, nesting material was observed being brought to the nests 2608 times, including 2560 sticks and 47 palm leaves, and grass was observed being taken into a nest chamber once. Only two of the sticks delivered were taken to a nest an individual did not occupy, and on both these occasions it was to a nest adjacent to their own. Birds were observed engaging in nest maintenance activities 1167 times.

Males were observed building more than females when we included all individuals (Figure 5.6a) and when we included only birds observed in one or the other year (both $p < 0.001$; Table 5.1a, b). Similarly, birds that were breeding in groups as opposed to pairs were observed engaging in less building work in both models (both $p < 0.05$; Table 5.1a, b; Figure 5.6c). The year of the observations influenced the amount of building behaviour observed with more building observed in 2018 than 2019 when all data was included, likely the result of a larger amount of time observing nests in 2018 ($p < 0.05$; Table 5.1a).

Males were observed maintaining the nest more than females when we included birds observed in both years and when only including birds observed once in the more conservative dataset (both p < 0.05; Table 5.1c, d; Figure 5.6b). However, there was no difference in the nest maintenance activity of birds that bred in groups compared with pairs (both p > 0.05; Table 5.1c, d; Figure 5.6d). We also observed more maintenance behaviour in 2018 than 2019, again likely a result of the larger amount of observation hours in 2018 (both p > 0.05; Table 5.1c, d).

Table 5.1. Negative binomial GLM examining factors affecting the observed numbers of building and nest maintenance events by individuals

Model	Parameter	Estimate ± SE	t	p
a) Nest building All individuals	(Intercept)	0.657 ± 0.147	4.466	< 0.001
	Sex	2.384 ± 0.155	15.426	< 0.001
	Year	-0.742 ± 0.137	-5.419	< 0.001
	Group member	-0.319 ± 0.146	-2.195	0.031
	*Group*sex*			*0.819*
b) Nest building Individuals observed in one year only	(Intercept)	0.265 ± 0.293	0.904	0.366
	Sex	2.376 ± 0.317	7.504	< 0.001
	Group member	-0.647 ± 0.274	-2.363	0.023
	Year			*0.244*
	*Group*sex*			*0.940*
c) Nest maintenance All individuals	(Intercept)	1.315 ± 0.115	11.428	< 0.001
	Sex	0.738 ± 0.132	5.588	< 0.001
	Year	-1.084 ± 0.131	-8.291	< 0.001
	Group member			*0.366*
	*Group*sex*			*0.596*
d) Nest maintenance Individuals observed in one year only	(Intercept)	1.049 ± 0.238	4.404	< 0.001
	Sex	0.668 ± 0.275	2.433	0.019
	Year	-0.688 ± 0.275	-2.502	0.016
	Group member			*0.800*
	*Group*sex*			*0.790*

a, c) Models including all individuals; N = 206 birds (83 female, 123 male, 139 in pairs, 67 in breeding groups). b, d) Individuals observed in only one year; N = 66 birds (25 female, 41 male, 39 in pairs, 27 in breeding groups). We present information on terms in the final models and those removed. Terms were considered significant at $p < 0.05$. Dropped terms indicated in italics. Effect sizes (± SE) were obtained from the minimal model in each case. We individually returned terms removed during model selection to the minimal model to assess significance using likelihood ratio tests, where appropriate also including individual terms from the interaction in this assessment.

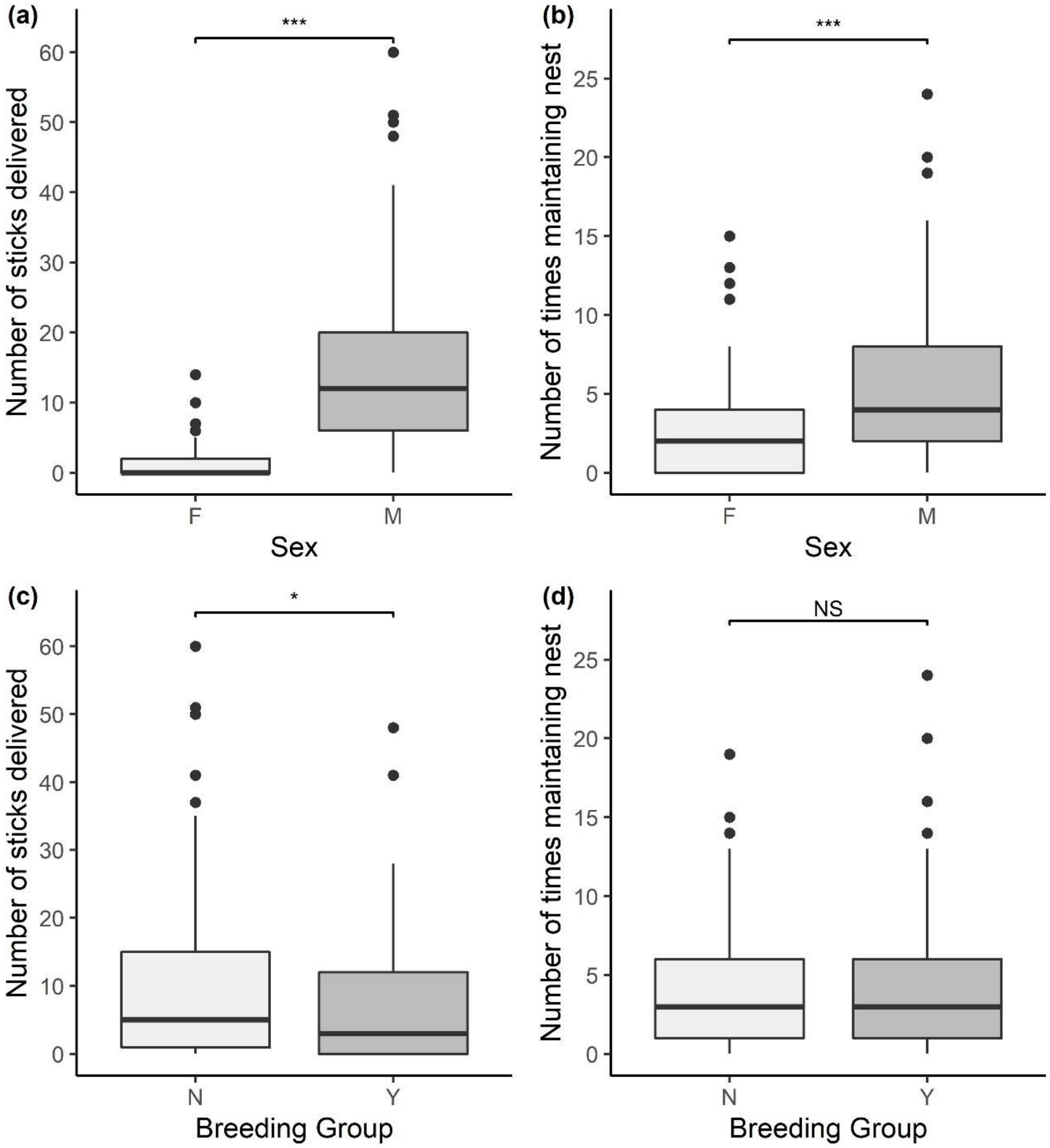

Figure 5.6. Nest building a) and maintenance b) behaviour of female (F) and male (M) monk parakeets. N = 206 birds (83 female, 123 male). Nest building c) and maintenance d) behaviour for birds in a breeding group (Y) and breeding pairs (N). N = 206 birds (139 in pairs, 67 in breeding groups). Data for all individuals shown for both years. Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots). ***$p < 0.001$, * $p < 0.05$.

5.4.2.2 Nest-building behaviour in breeding groups

To examine nest-building and maintenance behaviours within breeding groups, we focused on males because they contribute most building effort. There was variation between breeding groups in the contribution of different males. In some groups, a single male performed most building and maintenance effort while the other male(s) contributed very little, whereas in other groups effort was more evenly split. In 11/14 (79%) multi-male groups in which building was observed, all males engaged in building activity, while in the remaining 3/14 (21%) groups one male was not observed building. Similarly, in 12/13 (92%) multi-male groups in which nest maintenance was observed, all males contributed at least once. These results suggest that all males contribute to building and maintaining nests although effort may be split unevenly amongst group members.

5.4.2.3 Kleptoparasitism of nest material

Across both years, out of 2560 sticks delivered, 567 (22%) were successfully stolen from other nests and a further 180 unsuccessful attempts at stick theft were also observed. The great majority (90-98%) of thefts took place within the tree the thief nested in, only 2-10% involved theft from another (neighbouring) tree's nests. Only on two occasions were these stolen sticks not from the tree immediately adjacent to an individual's own nesting tree. Note that we assumed all sticks not directly observed being collected or stolen, that were brought to the nest from a distance, were collected rather than stolen, so it is possible we underestimated the amount of kleptoparasitism that occurs. For instance, birds were observed stealing from nests in trees up to 43 m from their own nest, therefore our estimate of the frequency of theft is conservative.

Males and females were both observed stealing nest material but males did so significantly more than females when we included all individuals ($p < 0.001$; Table 5.2a; Figure 5.7a) and when we just included birds observed in only one year rather than in both years ($p < 0.001$; Table 5.2b).

We also observed heterospecific kleptoparasitism of nesting material at our study site; grey herons, *Ardea cinerea*, stole nest material from monk parakeet nests on 69 occasions over the course of this study. On six occasions two herons stole sticks simultaneously from different nests in the same tree and on one occasion, three herons stole sticks from the same monk parakeet nest simultaneously, showing that multiple herons exploited this nesting material resource.

5.4.2.4 Nest defence

Birds were frequently observed defending their nests from kleptoparasites. Of the 194 nest defence events recorded, 172 (89%) prevented kleptoparasitism and on only 22 (11%) occasions were the thieves successful despite attempted nest defence. Most defence events involved a single bird chasing the thief (N = 182), but on 12 occasions two birds acted together; on six of these occasions the birds were confirmed as either pairs (N = 4) or from the same breeding group (N = 2). Multiple members of breeding groups were observed defending the nest, and may represent part of their investment in the shared breeding attempt. Males (N = 55 events) and females (N = 82 events) were observed defending nests, with females engaging in nest defence significantly more than males ($p < 0.01$, Figure 5.7b, Table 5.2c).

Table 5.2. Negative binomial GLM examining factors affecting the observed numbers stick theft by individuals and the numbers of nest defence events

Model	Parameter	Estimate ± SE	t	p
a) Kleptoparasitism All individuals	(Intercept)	-1.010 ± 0.291	-3.473	< 0.001
	Sex	2.551 ± 0.319	7.994	< 0.001
	Year	-1.038 ± 0.270	-3.838	< 0.001
b) Kleptoparasitism Individuals observed in one year only	(Intercept)	-1.061 ± 0.538	-1.974	0.048
	Sex	2.476 ± 0.607	4.080	< 0.001
	Year	-1.366 ± 0.559	-2.445	0.014
c) Nest defence All individuals	(Intercept)	0.396 ± 0.221	1.791	0.073
	Sex	-0.857 ± 0.277	-3.093	0.002
	Year	-1.175 ± 0.297	-3.951	< 0.001

a, c) Models including all individuals; N = 206 birds (83 female, 123 male). b) Individuals observed in only one year; N = 66 birds (25 female, 41 male).

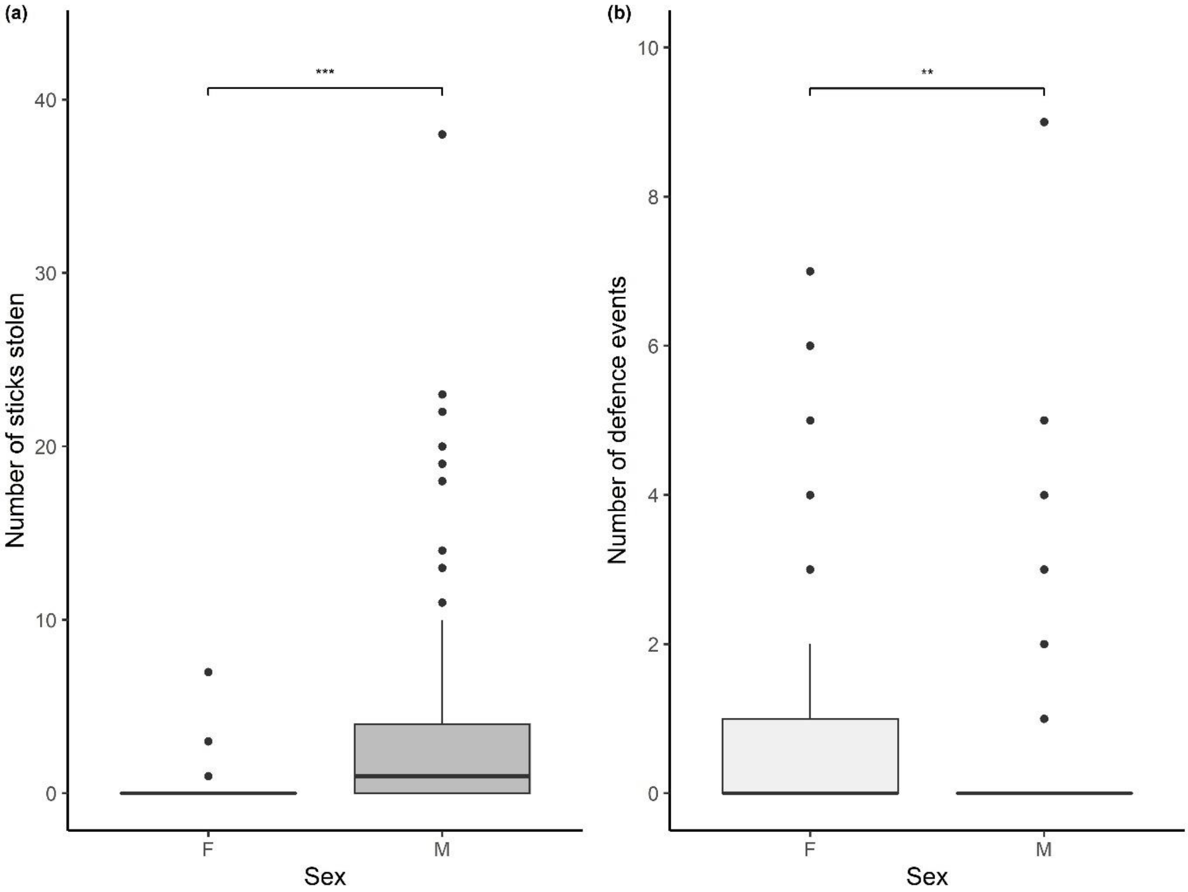

Figure 5.7. a) Stick theft and b) nest defence behaviour by female (F) and male (M) monk parakeets. Data for all individuals shown for both years (N = 206 birds, 83 female, 123 male). Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots). ***p < 0.001, **p < 0.01.

5.4.3 Productivity and reproductive investment

5.4.3.1 Clutch size and number of fledglings for pairs and groups

Clutch sizes did not differ significantly between pairs (mean = 6.2 ± 1.9, range = 1-16, N = 101) and groups (mean = 6.6 ± 3.3, range = 2-14, N = 27), nor between years (both p > 0.1; Table 5.3a; Figure S5.2a). There was no significant difference in the probability of fledging young between pairs and groups (p = 0.258; Table 5.3b) and similarly, the number of fledglings produced by pairs (mean = 2.7 ± 1.3, range 1-6) and groups (mean = 3 ± 1.5, range = 1-5) did not differ significantly (p = 0.548), although the number of fledglings was lower in 2019 (Table 5.3c; Figure S5.2b).

Table 5.3. Factors affecting clutch sizes and the number of fledglings, assessed using poisson GLMs and whether pairs or groups are more likely to produce fledglings assessed using binary logistic regression GLM

Model	Parameter	Estimate ± SE	t	p
a) Clutch size	(Intercept)	-1.877 ± 0.052	36.205	< 0.001
	Breeding group	0.067 ± 0.085	0.785	0.432
	Year	-0.103 ± 0.071	-1.457	0.145
b) Producing fledglings	(Intercept)	0.1650 ± 0.267	0.618	0.536
	Breeding group	-0.506 ± 0.447	-1.132	0.258
	Year	-0.374 ± 0.358	-1.045	0.296
c) Number of fledglings	(Intercept)	1.157 ± 0.102	11.294	< 0.001
	Breeding group	0.121 ± 0.202	0.601	0.548
	Year	-0.374 ± 0.358	-1.045	0.014

For (a) and (b) total N = 128 nests, 101 attended by pairs, 27 attended by breeding groups, (c) total N = 60 nests, 50 attended by pairs, 10 attended by groups.

The clutch sizes of multi-female groups (N = 6) tended to be larger than those of multi-male groups (N = 12; Z = -1.89, p = 0.059; Figure 5.8) suggesting that there was joint-nesting by females when groups contained more than one female.

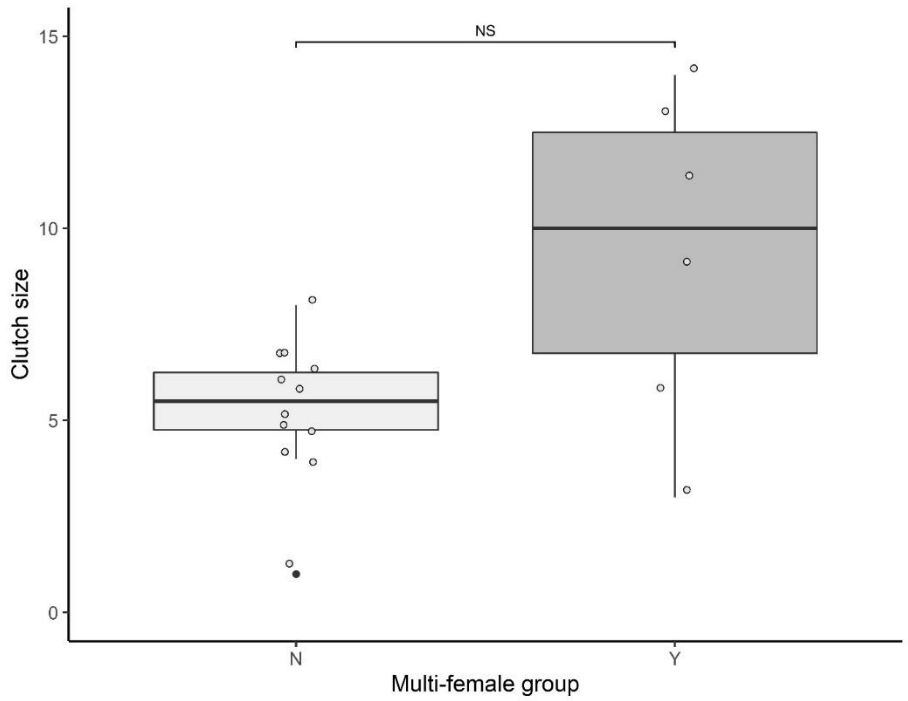

Figure 5.8 Clutch sizes in breeding groups, multi-female (N = 6 groups) and multi-male (12 groups). p = 0.059. Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

5.4.3.2 Provisioning behaviour in pairs and groups

Adults provision nestlings in the nest chamber by regurgitation, so nestling feeds could not be observed directly. However, assuming that birds without nest material entering nest chambers containing nestlings are provisioning young, the number of nest visits could be used to indirectly assess provisioning. Across both years we recorded 1407 nest visits satisfying these assumptions. In 2018, we observed nest visits by 104 marked birds (46 females, 58 males) with a mean number of nest visits per bird of 5.9 ± 4.8 SD (range 1- 31); in 2019, we observed visits by 85 marked birds (32 females, 42 males) with a mean of 2.5 ± 1.5 SD visits per bird (range from 1-7), including only those that were observed entering the nest at least once.

In 2018 and 2019, males (2018: N = 18, 2019: N = 16) and females (2018: N = 14, 2019: N = 12) from 26 different breeding groups were observed entering nests. In both years, multiple group members were observed entering nests; in 9/14 groups (64%) that contained at least three marked members, three or more birds were observed entering nests and were assumed to be feeding nestlings. These data indicate that multiple group members likely provision offspring.

We recorded 47 instances of fledglings being fed by adults, including feeds by males (N = 21 occasions) and females (N = 11 occasions). In the 26 cases where both fledgling and adult were identifiable, the fledgling was from the chamber that the adult was known to attend. Just 12 feeds were by adults from a group rather than a pair, and in none of these did we observe fledglings being fed by more than two marked members of the group, so we were unable to confirm that fledglings from groups are fed by all group members.

We also recorded begging by offspring to breeding group members, observing 26 incidents of offspring begging to adults from five breeding groups. In two groups, begging was directed at more than one group member, again suggesting that multiple group members provision offspring, although sample sizes are too small to draw any firm conclusions.

5.4.3.3 Copulations

We observed 18 copulations, nine involving known social pairs, and the remaining nine involved an unmarked bird, but in each case, the bird observed copulating with it was known to have an unmarked pair/group member. Six copulations involved members of breeding groups, but we saw no group members copulating with more than one other member of their breeding group.

5.4.3.4 Parentage

We examined paternity for 76 chicks in 22 broods raised by social pairs, and parentage of 23 chicks in five broods raised by groups. Across both years, brood sizes ranged from 1-9 nestlings (mean = 3.7 ± 1.8 SD, N = 27 broods).

Social pairs - In 2018, 2/23 (9%) chicks in 2/8 (25%) broods were likely to be the result of EPP, the remainder being assigned to the social male. In 2017, 13/53 (25%) chicks in 4/14 (29%) broods were considered to be the result of EPP, while in one brood (7%) there was evidence of possible intra-specific brood parasitism. The remaining 40 (75%) chicks were all assigned to their putative mother and father. It should be noted that, as mentioned above, observations were less intensive in 2017 and therefore parents may have been missed if they were part of a group, so cases of EPP or ISBP could have been offspring from an unidentified group member(s) in that year. Overall, across both years our analyses indicate social and genetic monogamy in 68% of broods raised by pairs; 27% of broods contained at least one chick resulting from EPP, and we recorded one case (4.5% of broods) of possible ISBP.

Breeding groups - Across both years we assessed parentage for five broods raised by groups. One group indicated a single breeding pair contributed to the breeding effort, whereas in the other four groups we detected either co-breeding pairs, more than one male breeding with a single female, two breeding females with either more than one male or unsampled parents (see *Relatedness within broods* for further information).

5.4.3.5 Relatedness within broods

Mean pairwise relatedness of chicks within all broods was 0.417 ± 0.192 SD (N = 187 dyads, 27 broods; range -0.191 to 0.809; Figure 5.9a, Figure S5.3), indicating a mixture of potentially unrelated individuals, half-siblings and full-siblings, as would be expected given the results from the parentage analysis and our assessment of the relatedness between the social siblings in breeding groups. Mean relatedness among all chicks within broods ranged from 0.163 to 0.640 again indicating a range of relationships between nestlings (Figure 5.9b). Pairwise relatedness was significantly higher amongst broods that showed no evidence of EPP or mixed parentage compared to those broods with at least one extra-pair offspring or evidence of mixed parentage ($p < 0.001$; Table S5.1; Figure 5.9a). In the case of apparently monogamous broods, it is notable that mean relatedness is close to that expected among full siblings ($r = 0.5$) There was no significant difference between mean relatedness within broods thought to have EPP/mixed parentage and those that did not ($Z = -1.680$, $p = 0.093$;

Figure 5.9b); however, this pattern may have been due to small sample sizes. Our results were further corroborated by maximum likelihood relationship estimations from ML-RELATE; with 65% (121 dyads) assigned as full-siblings or parent-offspring relationships (N.B. all comparisons were within broods, so parent-offspring is not a possible relationship, but this assignment indicates the close relatedness expected between full-siblings; Figure S5.4, S5.5). A further 28% (53 dyads) were assigned as half-siblings and 7% (13 dyads) were determined to be unrelated individuals (Figure S5.4). We also visually confirmed that patterns of pairwise relatedness matched well with estimated relationships (Figure S5.5). In sum, these patterns of relatedness among nestlings, closely match those found in parentage analyses.

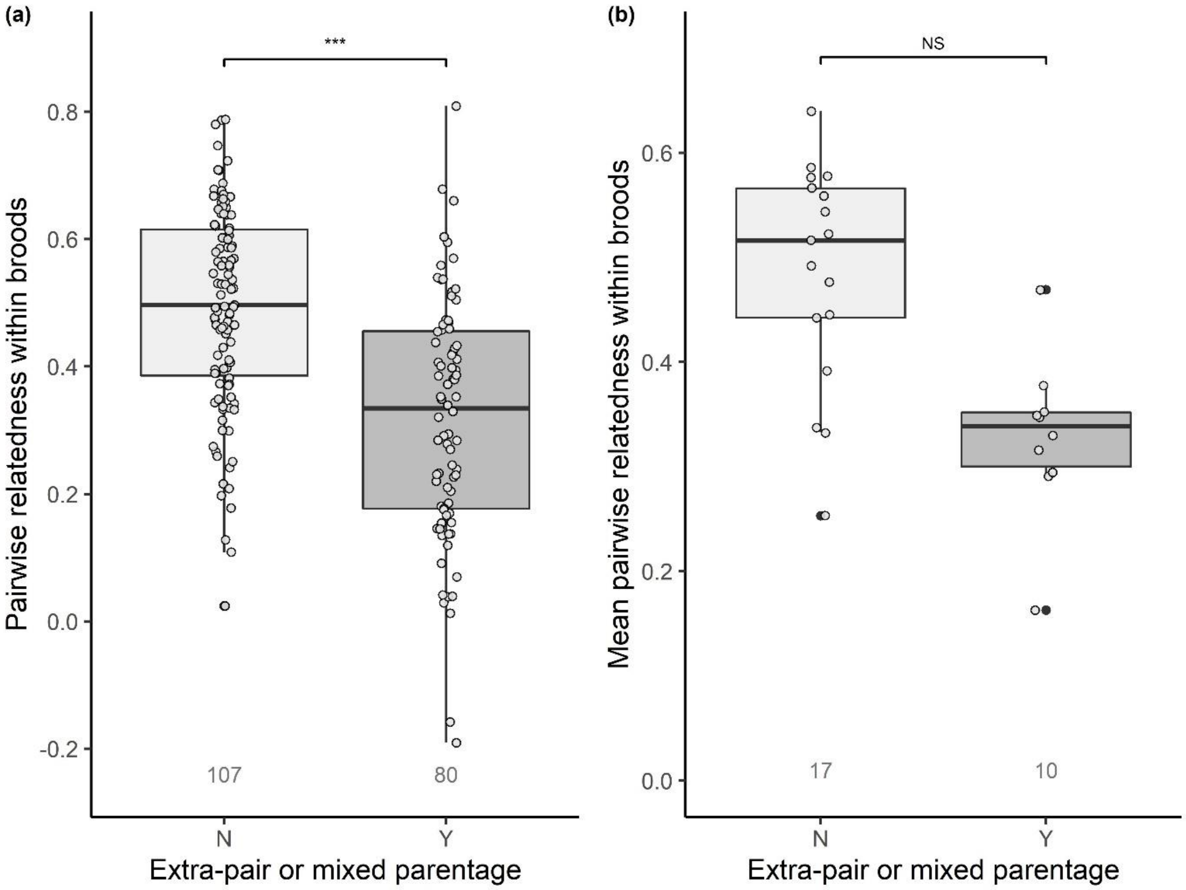

Figure 5.9. a) Pairwise relatedness between individuals within broods that showed extra-pair paternity or mixed parentage (Y) or indicated monogamous parents (N) and b) Mean pairwise relatedness within broods for both those that showed monogamy, and those that indicated an alternative parentage pattern. Boxplots indicate the interquartile range (box upper and lower limits),

median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots). Sample sizes indicated above the x-axis. ***p < 0.001.

5.5 Discussion

In monk parakeets, approximately 20% of the breeding attempts are made by groups of three or more individuals. These breeding groups are markedly diverse and flexible in size, sex-composition, age, genetic relatedness and the route taken to formation. Here, we presented evidence of groups forming through offspring retention, sibling coalitions and unrelated individuals aggregating together to make a breeding attempt. The diversity observed within monk parakeet breeding behaviour provides a potentially useful system to examine both the causes and evolutionary consequences of different routes to cooperation and points to a complex picture of the drivers of breeding associations in this species, with the potential for a number of indirect and direct benefits of forming breeding groups.

Individuals can gain indirect fitness benefits by increasing the production of related offspring (Hamilton, 1964). Such benefits may be accrued in the breeding groups reported here when they are composed of kin, for instance, where offspring were retained through their first breeding season or where individuals formed sibling coalitions and raised offspring together. Helping relatives is commonly reported in cooperatively breeding species (Hatchwell, 2009; Koenig & Dickinson, 2016), but we also presented evidence of unrelated birds associating in breeding groups. In these cases, there may be direct fitness benefits associated with forming breeding groups. For instance, nest building is an energetically expensive activity (Mainwaring & Hartley, 2013) and may be a particularly large energetic and temporal burden for the monk parakeet as their nests are maintained throughout the breeding season and the rest of the year (Eberhard, 1998) and can be very large; a nest in our study population that contained only two nest chambers was estimated to weigh 100 kg and contain approximately 10,000 sticks (J.C. Senar unpublished data). Living in groups may reduce the cost of nest-building, as we showed that individuals breeding in groups delivered less sticks to the nest compared to those in pairs, although the same pattern was not observed for nest maintenance behaviours. This may be indicative of the ‘load-lightening’ effects of extra group members where the workload is shared amongst larger numbers of individuals, and could result in increased survival (Meade et al. 2010) or lifespan (Downing et al. 2021). This ‘load-lightening’ effect may be of particular relevance to males as we showed that males engage most in nest-building during the breeding season. Another potential benefit of living in a group may be having more individuals to defend the nest from kleptoparasites, as we demonstrated that nest defence was effective against kleptoparasites and reduced loss of nest material. Our results show that the frequency of nest material kleptoparasitism is high and may present a significant challenge to nest maintenance. Larger groups may enable better defence of the nest, resulting in fewer incidences of theft and a lower burden of repairing damage to the nest. Nest defence could also reduce losses from heterospecific predators and the possibility of conspecific egg destruction by neighbours. Although we never observed egg destruction by conspecifics, egg destruction has been reported amongst neighbouring groups in other group breeding species, such as the greater ani, *Crotophaga major* (Almstead, Savagian, Smith, & Riehl, 2020), and could be a potential risk of breeding at the high densities observed in the monk parakeet. Alternatively, nesting in a group could result in conspecific egg destruction by other group members, resulting from reproductive competition, as has been observed in the acorn woodpecker, *Melanerpes formicivorus* (Koenig et al., 1995). There has also been speculation that adult monk parakeets occasionally kill nestlings (Peris & Aramburü, 1995), although this was not observed in our study population, so nest defence could also prevent this source of nestling mortality. There may also be direct benefits particularly for naïve individuals, for example, remaining with parents may allow for the opportunity to learn nest building and other relevant reproductive skills from experienced individuals (Langen, 1996), and allow sharing of the burden of nest building for young, naïve birds.

Questions remain regarding the construction of the unusual compound nest structure of the monk parakeet, particularly whether the nest is an emergent property of individuals investing building effort in their own nest chamber only, or whether structures are built and maintained through the cooperative investment of all nest occupants. Unlike another species that builds large communal nests, the sociable weaver, *Philetairus socius,* there is no obvious section of the nest (i.e. the thatch in sociable weavers; van Dijk et al., 2014) that would necessarily require cooperative investment in the monk parakeet. However, individuals were frequently observed delivering sticks to areas of the nest not immediately adjacent to the nest chamber they occupied (F.S.E.D.P. personal observation), which is indicative of some shared investment in the nest structure. In the sociable weaver, cooperative investment in the nest structure is kin-directed (van Dijk et al., 2014). Male kin are aggregated in the compound nests of monk parakeets (Dawson Pell et al., 2021), so there are several potential avenues of research into whether cooperation occurs in the construction and maintenance of such nests. Conversely, it is likely that there is also conflict over the construction of compound nests because we observed physical fights and vocalisations between resident birds and individuals that attempted to begin a new chamber on an existing nest (F.S.E.D.P. personal observation). Therefore, monk parakeets appear to demonstrate a degree of territoriality over their nest structure and newcomers are potentially not tolerated initially. It would be interesting to investigate further the balance of conflict and cooperation in compound nest construction in the monk parakeet.

We have previously demonstrated that kin are aggregated within nesting trees and compound nests at our study site, and dispersal is limited (Dawson Pell et al., 2021), therefore population viscosity may account for association of kin in breeding groups. However, for such associations to occur within the colonial, non-territorial social structure of monk parakeet populations while also enabling individuals to avoid the risk of inbreeding, kin recognition would likely be needed for individuals to reliably discriminate kin from non-kin (Cornwallis et al., 2009). In addition, the individuals that associated with a sibling in a coalition that dispersed and formed a breeding group would have been unable to assume individuals within their post-dispersal nesting tree were relatives, so it is likely some mechanism of kin-discrimination would be useful in such cases. We also showed that very few breeding pairs have relatedness exceeding that expected for 2nd order kin, suggesting that despite kin being aggregated within nests and nesting trees, individuals rarely pair with a 1st order relative for breeding and could be indicative of effective kin recognition in the monk parakeet. This is supported by previous work on this population that indicated no significant inbreeding at our study site, despite aggregations of relatives (Dawson Pell et al., 2021). In the monk parakeet, signatures of individual identity have been detected (Smith-Vidaurre, Araya-Salas, & Wright, 2020; Smith-Vidaurre, Perez-Marrufo, & Wright, 2021) that could facilitate such kin-discrimination, and investigations into whether such signatures of individual identity reflect patterns of genetic relatedness may be fruitful for our understanding of kin recognition in this species.

We examined a variety of behaviours that could contribute to the reproductive effort in breeding groups. First, we recorded defence against nest material kleptoparasitism, which could otherwise be a significant cost because up to 20% of sticks delivered to nests were stolen from another nest. Defending against such theft would be useful in maintaining nest integrity and function. Although the number of observations was not particularly high, we showed that in breeding groups multiple group members contribute to nest defence. Second, we showed that multiple members of breeding groups contribute to both nest building and maintenance, also key activities for the reproductive success of the group. However, there was notable variation in the building and maintenance efforts of individuals in groups, with some individuals contributing more effort than others. It would be an interesting avenue of future research to examine whether such effort is related to the share of paternity or relatedness within breeding groups.

Ideally, we would have liked to quantify the contributions of individuals in breeding groups to the feeding of offspring. However, there are a number of challenges associated with quantifying feeds in the monk parakeet. First, monk parakeets feed young by regurgitation, therefore we were unable to observe food items being brought to the nest. Second, monk parakeets could enter their nests for a number of reasons, so visits may not be indicative of feeding chicks; we did, however, use a conservative dataset that only included visits where nest material was not delivered and nest maintenance activities were not overt. In both years we observed multiple members of breeding groups of both sexes entering nest chambers, therefore it is possible that many individuals provision offspring in the nest when breeding in a group and strongly suggests that individuals share the provisioning effort for nestlings. It is also possible that nest visits could include other potentially beneficial behaviours, such as to incubate eggs, brood offspring or engage in other temperature regulating activities. We also observed feeding events once the offspring had fledged, however sample sizes were too small to allow meaningful conclusions to be drawn.

We found no significant differences in either clutch sizes or number of fledglings, between breeding pairs or groups, however, other reproductive benefits may have resulted from having additional group members that were not assessed here. For instance, there may have been increases in offspring condition or quality (e.g. te Marvelde et al., 2009; Bolopo et al., 2019), or in recruitment or survival probability (e.g. Preston, Briskie, & Hatchwell, 2016). There may also be other long-term reproductive benefits, such as increased lifetime reproduction (Barve et al., 2021) that result from breeding in groups. To gain a greater understanding of the fitness benefits and costs in this species lifetime fitness data would be fruitful. Our results are unlikely to be confounded by territory quality as monk parakeets are non-territorial and have home ranges that cover large areas of the study site (300-400 m) with many of the individuals nesting in close proximity with access to similar resources.

We presented evidence that multi-female groups tended to have larger clutch sizes than multi-male groups, although this trend did not reach statistical significance. This evidence of potential co-breeding by multiple females in a single nest was corroborated by our parentage analyses that suggested groups can have more than one male and more than one female contributing to the breeding attempt. Such co-breeding echoes that reported in the acorn woodpecker, in which up to three females nest jointly (Mumme, Koenig, & Pitelka, 1988), and the greater ani, in which up to four females share a nest (Riehl, 2011). Amongst parrots, the horned parakeet, *Eunymphicus cornutus*, has been observed joint nesting, although this involved only one nest (Theuerkauf et al., 2009).

We detected EPP in 27% of broods attended by social pairs at our study site, a lower overall estimate than that obtained in the native range (40% of chambers), although that estimate was not made in conjunction with nest observations (Martínez, De Aranzamendi, Masello, & Bucher, 2013). Mating patterns can differ between populations of the same species and promiscuity can be a context-dependent strategy (e.g. Indykiewicz, Podlaszczuk, & Minias, 2017), so mating patterns in the invasive range and native range could differ. Differences between populations in breeding behaviour can be marked, for instance, the reproductive capacity of monk parakeets is higher in the invasive range, with fledging success double that of the native range and the percentage of pairs attempting a second brood three times higher; in addition, despite no reports of one-year-old birds breeding in the native range, 55% of one-year-old birds bred at our study site (Senar et al., 2019). Monk parakeets nest at high densities, facilitating frequent social interactions and therefore the potential for extra-pair copulations. The proportion of broods with extra-pair offspring detected in this study echoes patterns seen in other colonially nesting birds, for instance, in black-headed gulls, *Larus ridibundus*, extra-pair offspring have been detected in 33% of broods (Ležalová-Piálková, 2011). However, a recent assessment of socially monogamous birds found no clear evidence that patterns of EPP can be explained by density (Brouwer & Griffith, 2019). There have been previous suggestions that there may also be intra-brood parasitism in the monk parakeet (Martínez et al., 2013), however, we have shown that in nests attended by groups, there may be chicks from different pairs of individuals leading to offspring that are unrelated within the same brood. This is an advantage of combining molecular analyses with detailed behavioural observations. It may be that previous reports of intraspecific-brood parasitism were in fact from nest chambers attended by groups of individuals, leading to the unrelated social siblings similar to those we observed in our study population.

The diversity of the monk parakeet breeding system revealed here precludes a simple definition; we have presented evidence of monogamy, EPP, co-breeding birds and breeders with possible helpers. Most parrots are considered monogamous (Forshaw, 1989; Cockburn, 2006), for example the

Bahama parrot *Amazona leucocephala bahamensis* (Walker, 2016), and cooperative breeding is typically considered rare amongst parrots and frugivores more generally (Arnold & Owens, 1998). However, there is a broad range of breeding systems reported in the Psittacidae, for instance systems of cooperative breeding with helpers have been described, such as the El Oro parakeet, *Pyrrhura orcesi* (Klauke, Segelbacher, & Schaefer, 2013), and female promiscuity with female only care of offspring with multiple males provisioning breeding females such as in the greater vasa parrot, *Caracopsis vasa* (Ekstrom et al., 2007), and the Seychelles black parrot, *Coracopsis barklyi* (Reuleaux et al., 2014). There are also systems of cooperative polyandry with care for offspring provided by both sexes, for example, up to seven males with a single female in the eclectus parrots, *Eclectus roratus* (Heinsohn, Ebert, Legge, & Peakall, 2007). Other systems involve joint nesting by potentially monogamous pairs such as that in the horned parakeet (Theuerkauf et al., 2009), and there are breeding systems characterised by lekking within the parrot family too, e.g. kakapo, *Strigops habroptilus* (Merton, Morris, & Atkinson, 1984). We are unable to characterise the monk parakeet breeding system neatly but have here highlighted the diversity of breeding behaviour in one population and our results add to our understanding of the breadth of the different breeding systems within the Psittacidae.

In conclusion, we have presented evidence of marked diversity and flexibility in the breeding behaviour of the monk parakeet. Although the majority of breeding attempts are made by social pairs, we demonstrated that around 20% of breeding attempts are made by groups. Groups are diverse in sex-ratios, ages and genetic relatedness and we found two clear routes to breeding group formation; retained offspring and sibling coalitions, although high relatedness between group members is not required for group formation. Productivity didn’t differ between groups and pairs, but evidence from clutch sizes and patterns of genetic relatedness indicate joint nesting attempts. There are several avenues of research which could stem from our findings that may be fruitful, including investigations into kin-discrimination mechanisms and investment by group members in relation to whether they are co-breeding and their share of parentage within the brood. In general, our results add to the limited knowledge of parrot breeding behaviour, and breeding systems such as that described here may be particularly useful to address the causes and evolutionary consequences of various routes to cooperation.

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5.6 Supplementary material for:

Flexible social organisation and breeding system of a social parrot revealed by genetic analysis

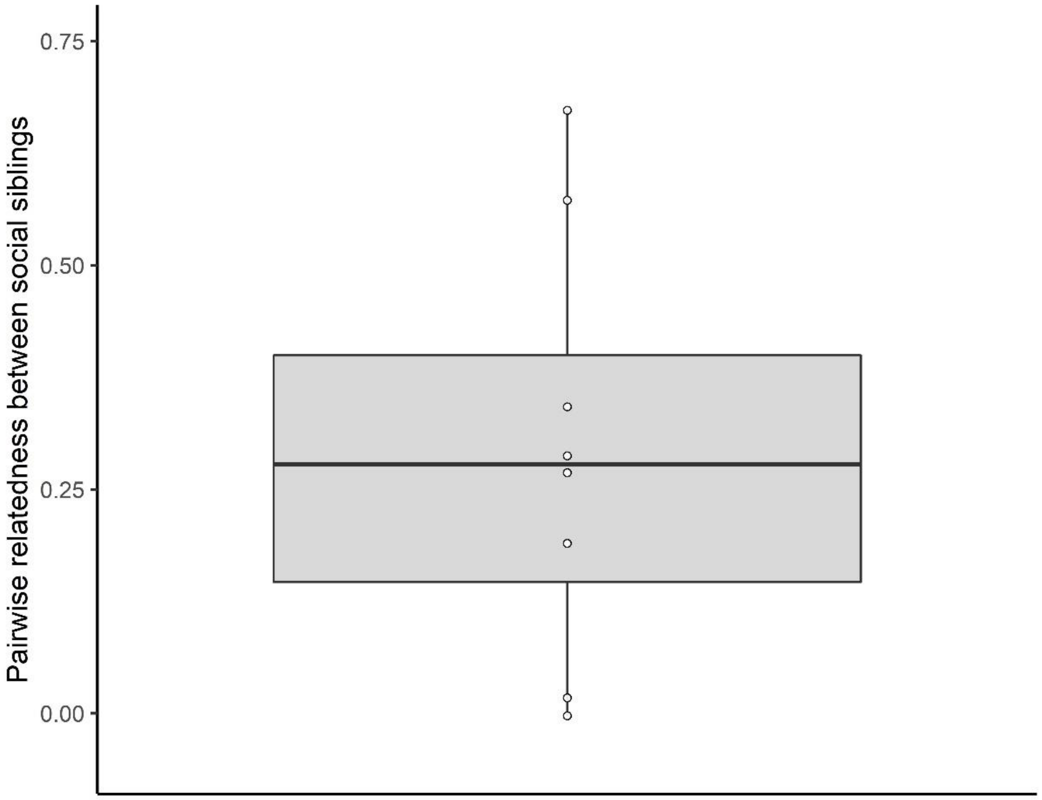

Figure S5.1. Pairwise relatedness between social siblings in breeding groups (N = 8 social sibling comparisons). Boxplots indicate: the interquartile range (box upper and lower limits), median relatedness values (thick lines within boxes), minimum and maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

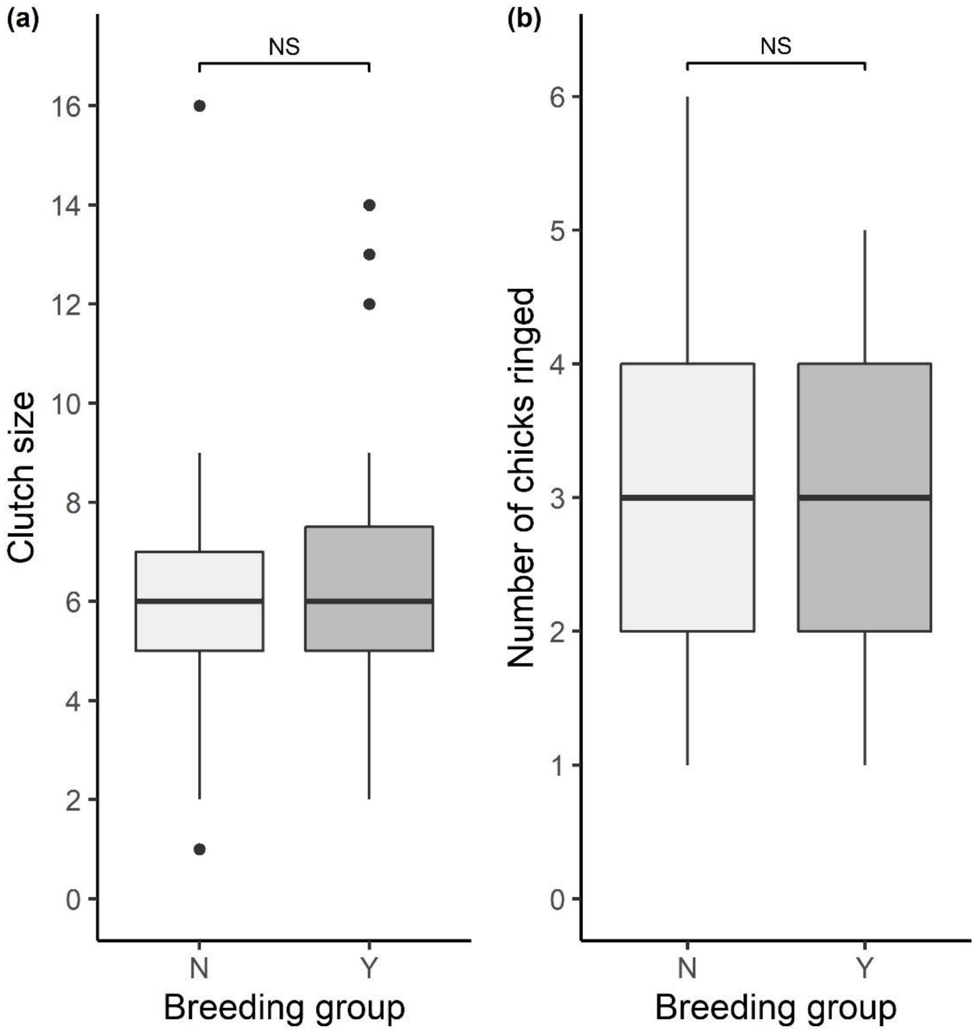

Figure S5.2. a) Clutch size (N = 128 nests, 101 attended by pairs, 27 attended by breeding groups) and b) number of chicks ringed (N = 50 pairs, N = 10 groups) for nests attended by pairs (N) and breeding groups (Y). Data for both 2018 and 2019 shown. Both $p > 0.4$. Boxplots indicate: the interquartile range (box upper and lower limits), median relatedness values (thick lines within boxes), minimum and maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

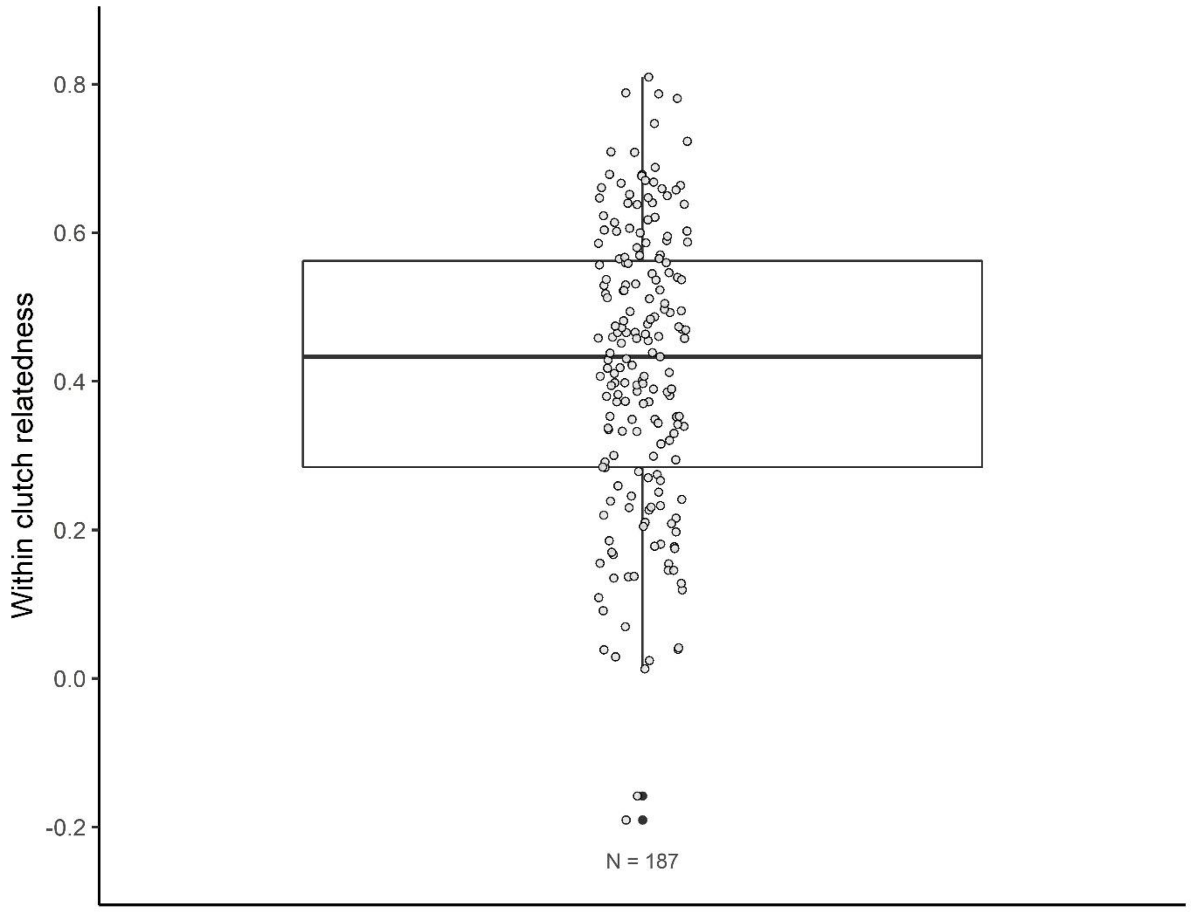

Figure S5.3. Pairwise relatedness within clutches, N = 187 comparisons. N = 27 clutches. Data shown for clutches in 2017 and 2018. Boxplots indicate: the interquartile range (box upper and lower limits), median relatedness values (thick lines within boxes), minimum and maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

Table S5.1. Linear mixed model examining factors affecting the relatedness between nest-mates

	Fixed effect	df	Estimate ± SE	X^2	p
	(Intercept)		0.486 ± 0.020		
	EPP/mixed parentage	1	-0.170 ± 0.032	17.541	< 0.001
Random term	Brood ID		*0.002 ± 0.040*		

Variance (±SD) given for the random term is in italics. N = 187 dyads.

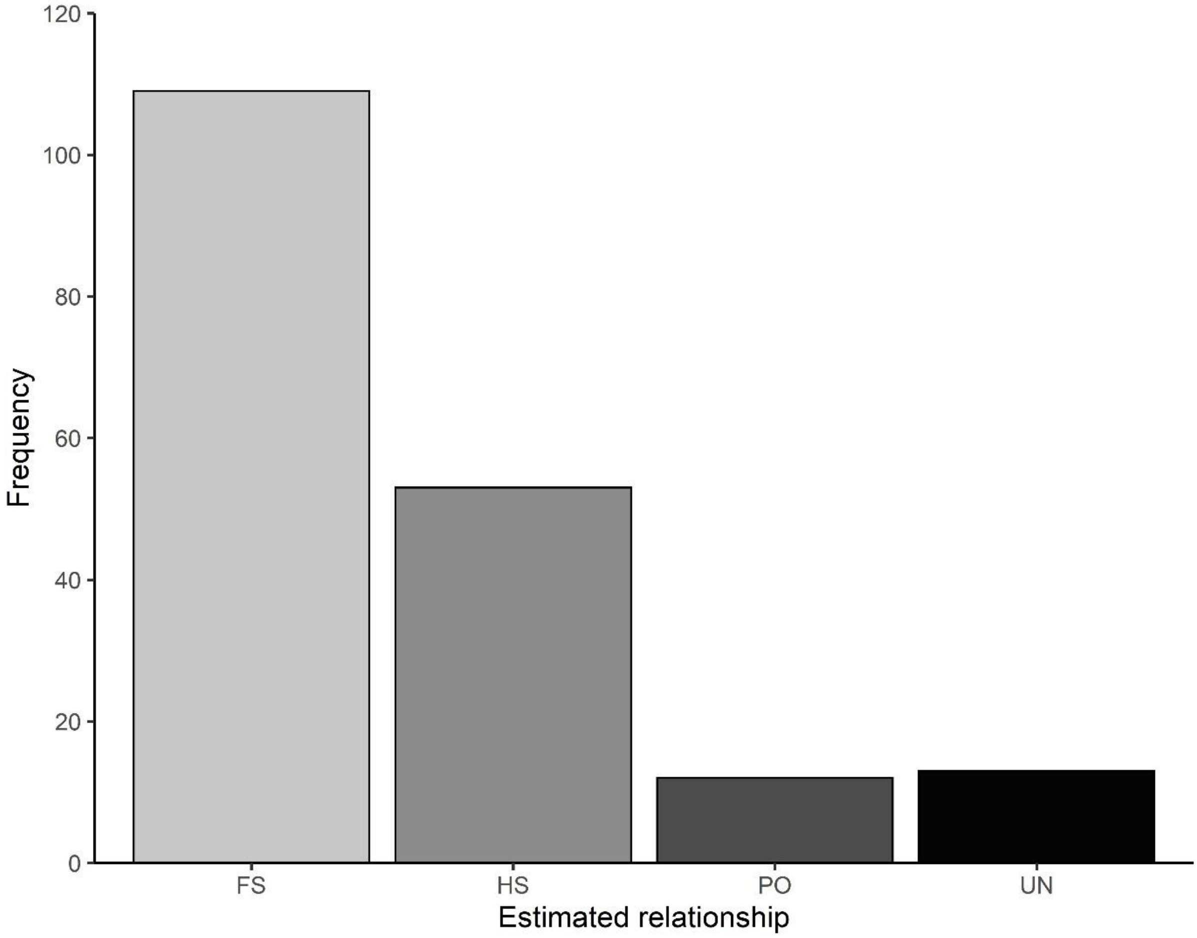

Figure S5.4. Frequencies of estimated relationships between nest-mates using maximum likelihood estimates from ML-RELATE (Kalinowski et al., 2006). Estimated relationships: FS – full-sibling, HS – half-sibling, PO – parent-offspring, UN – unrelated. N.B. As all comparisons were within broods, parent-offspring is not a possible relationship, however, it indicates close relatedness between individuals and these are likely full-sibling relationships.

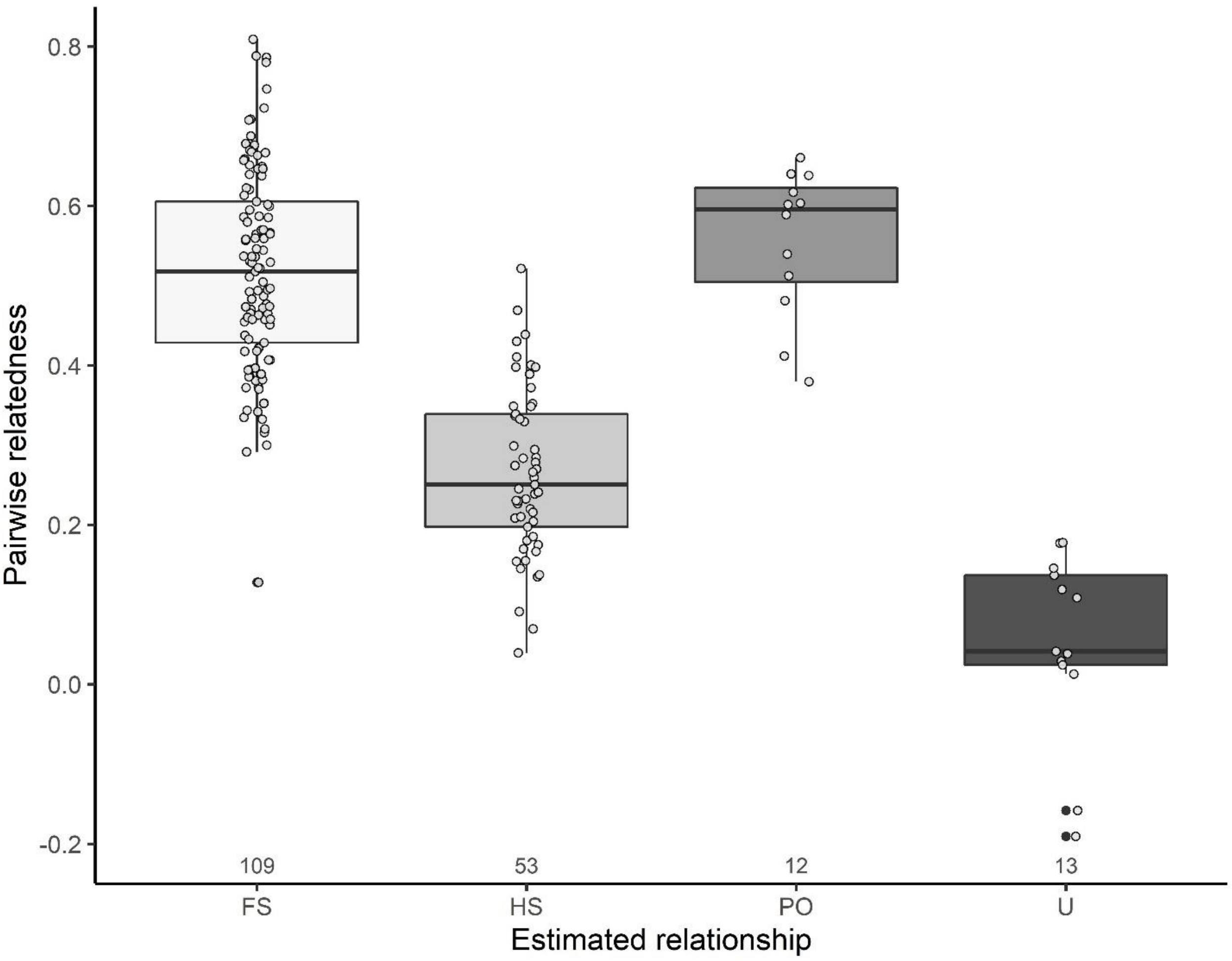

Figure S5.5. Maximum likelihood relationships estimated in ML-RELATE (Kalinowski et al., 2006) compared to pairwise relatedness estimates made in SPAGeDI (Hardy & Vekemans, 2002). Number of estimated relationships indicated above the x-axis. Estimated relationships: FS – full-sibling, HS – half-sibling, PO – parent-offspring, U – unrelated. N.B. As all comparisons were within broods, parent-offspring is not a possible relationship, however, it indicates close relatedness between individuals and these are likely full-sibling relationships. Boxplots indicate: the interquartile range (box upper and lower limits), median relatedness values (thick lines within boxes), minimum and maximum values excluding outliers (lines extending from boxes) and outliers (filled dots).

6. Social associations are predicted by nest proximity, but not kinship in a free-living social parrot

6.1 Abstract

An individual's social associations are often non-random and can have important fitness consequences. However, social behaviour and the drivers of social associations are relatively understudied in parrot species due to methodological challenges of studying parrots in the field. Here, we combine field observations with molecular genetic techniques and social network analysis to investigate the drivers of social associations in free-living monk parakeets, *Myiopsitta monachus*. The monk parakeet is a non-territorial parrot species that constructs large stick nests that are often closely aggregated, with relatives spatially clustered to form kin neighbourhoods. First, we investigated whether nest proximity or genetic relatedness influence social associations away from the nest. We found that social associations are relatively weak between adults during the breeding season, with a limited number of strong social ties. Association strengths decreased with increasing inter-nest distance despite large home range sizes, a result that may be explained by either shared space use or by individuals preferentially associating with familiar birds away from the nest. In contrast, there was negligible influence of genetic relatedness on the strength of social associations when foraging despite relatives being clustered within compound nests and nesting trees. These patterns were qualitatively similar when examining same-sex and opposite-sex social associations separately. Secondly, we investigated whether breeding pair members were close social associates, finding that in 66% of cases an individual's closest associate was their social mate, although social bonds also exist outside of the pair. Members of breeding groups were also regularly close social associates when foraging, although group members were amongst each other's closest associates less frequently than social pairs. Our results add to the limited knowledge of the drivers of social associations in free-living parrots and have implications for our understanding of social behaviour in this unusual parrot species.

Keywords: Social associations, monk parakeet, *Myiopsitta monachus*, genetic relatedness, nest proximity, parrots, space use

6.2 Introduction

Associations within populations or groups of animals are often non-random, with individuals associating preferentially with certain group members (e.g. Whitehead, 2008). The social connections between individuals and the resulting network structure can have wide-ranging implications for a variety of ecological and evolutionary processes (e.g. Firth, Voelkl, Farine, & Sheldon, 2015). For example, social structure can have consequences for sexual selection and mating strategies (Oh & Badyaev, 2010), can determine how information spreads through a group or population (Franz & Nunn, 2009; Firth, Sheldon, & Farine, 2016) and, similarly, can determine the spread of disease or parasites through a network of connected individuals (Hamede, Bashford, McCallum, & Jones, 2009; Rimbach et al., 2015; Sah, Mann, & Bansal, 2018). Social associations can also influence fitness (Royle, Pike, Heeb, Richner, & Kölliker, 2012), for instance by impacting survival chances (Stanton & Mann, 2012; Ellis et al., 2017) or reproductive success (Frère et al., 2010; Riehl & Strong, 2018).

There are a number of factors that can underlie an individual's choice of social associates. One factor that can have an important influence on associations is kinship; preferentially associating with kin has been demonstrated in a variety of taxa including fish (e.g. Fraser, Duchesne, & Bernatchez, 2005), mammals (e.g. Gaspari, Azzellino, Airoldi, & Hoelzel, 2007) and birds (e.g. Kurvers et al., 2013). For instance, kinship is an important factor determining social structure in the Australian bottlenose dolphins, *Tursiops cf. australis* (Diaz-Aguirre et al., 2019) and kinship influences affiliative social interactions in the ring-tailed coati, *Nasua nasua* (Hirsch, Stanton, & Maldonado, 2012). In contrast, despite the presence of kin in the population, neither male or female common raccoons, *Procyon lotor*, preferentially associate with relatives (Hirsch, Prange, Hauver, & Gehrt, 2013) and kinship does not explain social associations in the black-and-white ruffed lemur, *Varecia variegate*

(Baden, Webster, & Bradley, 2020). Inclusive fitness theory predicts that by associating with kin, individuals can accrue inclusive fitness benefits (Hamilton, 1964). Preferential association with kin could increase an individual's fitness in a variety of ways, from sharing ecologically relevant knowledge leading to reduced foraging interference (Jarman, 1991), and increasing territory sharing and reducing time for food patch acquisition (Griffiths & Armstrong, 2002), to predator protection through alarm calling (Sherman, 1977), and aid rearing offspring (Pusey & Packer, 1994).

Another factor that can influence social associations is familiarity. Familiarity can result from shared use of space, for example in eastern grey kangaroos, *Macropus giganteus*, social association is more strongly correlated with space use than it is with kinship (Best et al., 2014). In addition, individuals may also be familiar to each other if they were raised together as juveniles; for instance, Trinidadian guppies, *Poecilia reticulata*, show a social preference for familiar individuals they were raised with (Griffiths & Magurran, 1999). Associating with familiar individuals can provide fitness benefits by increasing reproductive coordination and reducing competition (Riehl & Strong, 2018), or enhancing predator avoidance (Griffiths, Brockmark, Höjesjö, & Johnsson, 2004). Notably, multiple drivers of social association may act together to determine social structure, for instance, both familiarity and kinship determined preferred social associates during foraging in barnacle geese, *Branta leucopsis* (Kurvers et al., 2013).

In this study, we examined the social structure and associations of the monk parakeet, *Myiopsitta monachus,* and investigated two potential drivers of the observed associations. Monk parakeets are unique amongst parrots in that they build their own stick nests as opposed to breeding in natural cavities (Forshaw, 1989; Eberhard, 1998; Spreyer & Bucher, 1998). Their nests vary in size from single chambers to compound nests with several pairs or groups using separate nest chambers within a larger shared nest structure (Forshaw, 1989). These nests are often aggregated within nesting trees (Bucher, Martin, Martella, & Navarro, 1990; Eberhard, 1998). Previous investigations have revealed that monk parakeets live in ‘kin neighbourhoods’ with relatives aggregated within both shared compound nests and nesting trees (Dawson Pell et al., 2021).

In addition to the shared compound nests and nest aggregations, monk parakeets also display social behaviour away from the nest, foraging in flocks throughout the year. There is some evidence from unmarked wild flocks and marked captive individuals that pairs are the fundamental social unit in monk parakeets (Hobson, Avery, & Wright, 2014). Flocks of two individuals are reportedly the most common both in captivity and in the wild (captive: 25.2-30.4%, wild 32.3% of total flocks), however, flocks of > 60 individuals have been observed in the wild (Hobson et al., 2014). Captive birds have also been shown to display strong preferences for associating with certain individuals, forming strong bonds between pairs of individuals (Hobson et al., 2014) as well as amongst a small number of trios in captivity (Hobson et al., 2014). However, a detailed investigation into the patterns of social associations and the drivers behind social ties in free-living monk parakeets has not been conducted. Notably, social structure and the drivers of social associations are relatively understudied in the Psittacidae due to the methodological challenges of studying most parrot species in the wild, with many species being canopy-dwelling and not amenable to observation.

The kin neighbourhood social system, aggregated nests and social foraging behaviour of the monk parakeet make it an ideal species to examine the influence of kinship and familiarity through nest proximity on the social associations of foraging birds. Monk parakeets often forage on the ground, making observations of social groups more tractable than for most parrot species. The aim of this study was to combine molecular genetic techniques with field observations to first examine the overall pattern of social associations in the monk parakeet and then investigate whether the strength of monk parakeet social associations is reflective of either nest proximity or genetic relatedness. We also sought to examine whether social pairs and members of breeding groups were close social associates away from the nest. Through these investigations we aim to expand our understanding of the influence of kinship and familiarity on patterns of social association in this unusual parrot species and add to the limited knowledge of parrot social systems.

6.3 Materials and methods

6.3.1 Study site and species

The field study was conducted in the city of Barcelona, Spain (41.39°N 2.17°E) on the north-east coast of the Iberian Peninsula. The metropolitan area of Barcelona is approximately 102 km^2 and consists mainly of highly developed urban environment with numerous parks throughout the city. The main study site encompassed Ciutadella Park (a large central park of approximately 30 ha containing both native and exotic vegetation) and small parks and streets in the surrounding area up to approximately 2 km away (for a list of survey locations see Supplementary Material 6.6, S1).

The monk parakeet is a medium-sized parrot species native to South America that has become an invasive species around the world (Forshaw, 1989; Bush, Baker, & Macdonald, 2014; Russello, Avery, & Wright, 2008). Monk parakeets were first reported breeding in Barcelona in 1975 (Batllori & Nos, 1985) and now exist at some of the highest densities found in Europe. Population estimates in 2015 suggested around 5000 individuals were present in the city (Molina, Postigo, Román-Muñoz, & Del Moral, 2016; Senar, Montalvo, Pascual, & Arroyo, 2017). As a generalist forager, monk parakeets can be observed feeding in both trees and on the ground (Forshaw, 1989; Aramburú 1997; Bucher and Aramburú 2014; Borray-Escalante et al., 2020) and are highly visible for observations.

For detailed investigations into social associations, individuals must be uniquely identifiable (Whitehead, 2008). Birds were trapped for marking either in the nest as nestlings or incubating adults, using a baited food trap or gas-propelled nets. Approximately 62-64% of the study population are marked at any time, based on the proportion of individuals marked in 10 mature pine trees subjected to intense monitoring during the field season (Chapter 5). Birds have been ringed in our study population every year since 2002 and ringing effort involves two six-week sampling periods in the winter and summer months (Conroy & Senar, 2009). Monk parakeets in our study population are ringed with aluminium leg rings and marked with unique, light-weight medals attached to neck collars (Senar, Carrillo-Ortiz, & Arroyo, 2012). These medals are visible through binoculars up to 30-40 m distance and allow individual identification without the need for recapture. For birds first caught as adults, we use the year of ringing to determine the minimum age of an individual.

6.3.2 Compliance with ethical standards

Birds were handled and blood samples taken with special permission EPI 7/2015 (01529/1498/2015) from Direcció General del Medi Natural i Biodiversitat, Generalitat de Catalunya, following Catalan regional ethical guidelines for the handling of birds. JCS received special authorization (001501-0402.2009) for the handling of animals in research from Servei de Protecció de la Fauna, Flora i Animal de Companyia, according to Decree 214/1997/30.07. Handling times were kept to a minimum.

6.3.3 Identifying group members

Ciutadella Park and the other parks visited during this study are public access parks and monk parakeets are habituated to human presence near their nests and during foraging and other activities. We observed monk parakeet social groups away from the nest throughout the breeding season (March-September; Senar et al., 2019) in 2018 and 2019. Groups were recorded in one of two ways. First, groups of monk parakeets were recorded opportunistically when encountered during surveys of the field site. Groups were recorded engaging in a variety of activities including foraging, drinking, bathing and resting. Individuals were recorded in the same group if they were within approximately 5 m of each other. We used the ‘gambit of the group’, which assumes that all individuals in a spatially and/or temporally clustered group are associated with one another (Whitehead & Dufault, 1999). Any individuals that joined the group within approximately 2 minutes of the observer encountering the group were included as group members. GPS coordinates of each group were recorded along with the date and time. Secondly, groups were recorded during observations made at a baited trap (containing peanuts and sunflower seeds), situated on the roof of the Museu de Ciències Naturals within Ciutadella Park. For observations at the trap an observer situated inside the museum used binoculars to identify marked birds using the food trap in groups. These observations were conducted for approximately three hours a week throughout the breeding season. Marked birds were recorded at 10 minute intervals during the periods of observation at the trap, and as during surveys of the park, any individuals that joined the group at the trap within approximately 2 minutes of the observation starting were included in that flock.

6.3.4 Genotyping

Blood samples (maximum 100 µl) were taken during ringing of adults and nestlings for genetic sex-typing (monk parakeets are sexually monomorphic (Forshaw, 1989)) and to assess genetic relatedness between individuals. For details of blood sample storage and DNA extraction techniques see Dawson Pell et al. (2020). Individuals were initially typed following the same PCR protocols as described in Dawson Pell et al. (2020), using 26 microsatellite markers optimised in six multiplexes, with alleles all scored blind to bird identity and sex. Following assessment of marker quality, five loci were removed and not included in further analyses, resulting in 21 polymorphic microsatellite loci for our analyses: Mmon01, Mmon02, Mmon03, Mmon04, Mmon07, Mmon09, Mmon10, Mmon11, Mmon13, Mmon14, Mmon15, Mmon16 (Dawson Pell et al., 2020), MmGT060, MmGT046, MmGT105, MmGT030, MmGT071, MmGT057 (Russello, Saranathan, Buhrman-Deever, Eberhard, 2007), TG03-002 and TG05-046 (Dawson et al., 2010), and CAM-20 (Dawson et al., 2013). For further details of protocols and marker quality assessment see Dawson Pell et al. (2021). Individuals were sex-typed using the sexing marker Z002B (Dawson, 2007). A previous estimate of genotyping error, based on the repeat genotyping of 50 individuals with these markers in this study system is 3.1% (F.S.E.D.P. unpublished data).

6.3.5 Pairwise genetic relatedness

We calculated pairwise genetic relatedness between individuals using Queller and Goodnight's (1989) coefficient of relatedness (r_{QG}) in SPAGeDi version 1.5 (Hardy & Vekemans, 2002). We used the genotypes of all 142 unique individuals included in our social analysis to generate allele frequencies.

6.3.6 Nest locations and inter-nest distances

Nesting tree locations were determined in two ways. First, we conducted detailed behavioural observations at 10 large, mature pine trees in Ciutadella Park throughout the breeding season in 2018 and 2019. A total of 387 hours of observation were undertaken across the two seasons (2018: 263 hr, 2019: 124 hr); 113 marked individuals were located in these focal trees in 2018 and 103 marked birds in 2019. Birds were never observed to enter a nest chamber they were not using for breeding or roosting during our period of observation, so we are confident that birds assigned as nest occupants are residents in that nest and nesting tree. Second, we also conducted surveys in the rest of Ciutadella Park and in monk parakeet nesting areas up to 6 km from the park. These observations totalled 380 hours over the breeding seasons in 2018 and 2019. Once nests were located, we recorded the GPS coordinates of the nest. All individuals within a nesting tree were assigned the same GPS coordinates and were therefore recorded as having 0 m between their nests. GPS coordinates were converted to Cartesian coordinates (UTM) for calculations of inter-nest distance in SPAGeDi version 1.5 (Hardy & Vekemans, 2002). We calculated inter-nest distances separately for 2018 and 2019.

6.3.7 Social associations

Using flock co-membership, we calculated association indices using the simple ratio index (SRI; Cairns & Schwager, 1986) in R version 4.1.1 (R Core Team, 2018). The simple ratio index is used to estimate the strength of a social association between individuals and varies between 0 and 1, with 1 indicating that individuals are always observed together and 0 indicating two individuals have never been observed associating. The simple ratio index is calculated using the following equation:

$$\mathrm{SRI}_{AB} = x / (x + y_{AB} + y_A + y_B)$$

In which the SRI between the individuals *A* and *B* is defined as the number of observations in which the two co-occurred (x), divided by the number of observations in which they both occurred together or individually, with y_{AB} representing the occasions the individuals were observed simultaneously but apart and y_A indicating occasions that individual *A* was observed without individual *B* and y_B indicating the reverse.

In order to minimise any bias in association indices caused by limited sampling, we excluded birds observed on less than five occasions (2018: N = 171 birds excluded out of 364 sighted individuals; 2019: N = 131 birds excluded out of 288 sighted individuals). In addition, we excluded individuals that had fledged during that same breeding season, as these birds are still fed by parent birds and are therefore likely to be in association with parent birds away from the nest (2018: N = 74 fledglings excluded; 2019: N = 46 fledglings excluded).

6.3.8 Social associations, inter-nest distance and pairwise genetic relatedness

Based on recent developments in the field, we elected to use multi-membership models without permutations for our dyadic analysis (Franks et al. 2021; Hart et al. 2021; Weiss et al. 2021). To investigate whether social association strengths were reflective of inter-nest distance or pairwise genetic relatedness we fitted Bayesian multi-membership regression models in Stan (Stan Development Team 2020a) via RStan (Stan Development Team 2020b) using the brms package (Bürkner, 2017) in R version 4.1.1. We included the dyads as a multi-membership terms to account for undirected dependencies in allowing the dyad to be a member of both nodes. For this model, we used a binomial likelihood with association strength (SRI) as the response, and our predictor variables were pairwise genetic relatedness and inter-nest distance. Both our predictor variables were transformed to z scores before being used in the model. We applied weakly regularizing priors in these models. Our models were fit over 4 independent chains with a warmup of 3000 followed by 6000 iterations of sampling. We ran models separately for the data collected in each of the breeding seasons in 2018 and 2019.

Some dyads had data for inter-nest distance only, or relatedness only; these birds were removed before the brms analyses. Using data collected in 2018, including data collected at the food trap, we checked for any bias in those dyads removed for missing data through data visualisation. We plotted dyads with only one data point for either relatedness or inter-nest distance against SRI, and also plotted the full dataset that included no individuals with missing data to determine whether there was any bias in those removed (Figure S6.1). We could not visually detect any bias in removed dyads, indicating that data was missing at random, so we proceeded with the dataset that includes only dyads with complete data.

In 2018, once the minimum sightings limit was applied, we had data on 821 social groups for analysis. A total of 110 individuals (41 females, 69 males, 5995 dyads) were observed more than five times, and had both genetic and nest location information available. The mean number of observations per bird in 2018 was 17.0 ± 7.8 SD, with females (13.9 ± 7.0, median = 13) being observed less than males (18.8 ± 7.7, median = 18; Wilcoxon rank sum test: $Z = -3.28$, $p = 0.001$; Figure S6.2a). Our dataset included birds aged from 1-12+ years old based on the year of ringing or the fledging date. In 2019, we had data on 753 social groups and there was a total of 82 individuals (32 females, 50 males, 3403 dyads) that met the criteria for inclusion with ages ranging from 1-13+ years old. The mean number of observations per bird in 2019 was 15.9 ± 7.8 SD and males (18.7 ± 7.4, median = 19) were again observed more than females (11.5 ± 6.4, median 9.5; $Z = - 4.33$, $p < 0.001$; Figure S6.2c).

We regenerated the social association matrices and re-ran our analyses described above having removed the data collected at the baited trap in both 2018 and 2019 in case this large, artificial food source was drawing birds from greater distances, and perhaps resulting in more individuals being socially associated. When data from the food trap was excluded, we had data from 656 observed social groups and 98 individuals (33 females, 65 males) that met the inclusion criteria in 2018, and from 680 social groups and 78 individuals (29 females, 49 males) in 2019. Age ranges were the same as above for both years. The mean number of observations in 2018 was 12.5 ± 5.5 SD and in 2019 was 15.4 ± 7.4 SD. When we excluded data from the trap we found no differences between the number of observations per female and male in 2018 (female mean ± SD; 11.5 ± 5.4, median = 11, male mean ± SD; 13.0 ± 5.5, median = 13; Z = -1.30, p = 0.19; Figure S6.2b). However, in 2019 males were observed more than females when the data from the trap was excluded (female mean ± SD; 11.4 ± 6.4, median = 10, male mean ± SD; 17.7 ± 6.9, median = 19; Z = - 3.91, p < 0.001; Figure S6.2d).

6.3.9 Same-sex and opposite-sex associations

Using the 2018 dataset including observations recorded at the food trap, we ran the same model described above separately for female-female (N = 820 dyads), male-male (N = 2346 dyads), and opposite-sex (N = 2829) associations to investigate whether the drivers of social associations were similar for same-sex and opposite-sex dyads. The 2019 dataset had too few female-female dyads to repeat this analysis for the second year.

6.3.10 Associations between social pairs and breeding group members

In captive populations of monk parakeets, individuals tend to form strong social associations with a single individual (Hobson et al., 2014). We assessed whether social pairs were each other's closest social associates when away from the nest using the full datasets from 2018 and 2019. In addition, approximately 20% of the breeding attempts made by monk parakeets at our study site are made by groups of three or more birds (Chapter 5), we therefore also examined whether breeding group members were close associates when away from the shared nest. We used data collected for a concurrent study into breeding behaviour (Chapter 5) to identify social pairs and breeding groups that were also present in our social association data. In brief, pairs and groups were identified during behavioural observations at 10 focal pine trees that totalled 387 hours across the breeding seasons of 2018 and 2019. We only included groups in which all members were marked and also met the inclusion criteria for our social network. For both social pairs and breeding groups we determined the top 10 social associates, ranked by social association strength (SRI) to assess whether members of pairs and social groups preferentially associate with each other away from the nest.

6.4 Results

6.4.1. Characteristics of monk parakeet social associations

Social association strengths between individuals were relatively sparse and weak in both years (Figure 6.1; Figure 6.2). Mean SRI ± SD was 0.02 ± 0.04 for 110 birds in 2018 (N = 5995 possible dyads), and 0.02 ± 0.04 for 82 birds in 2019 (N = 3403 possible dyads). In both years, distributions of associations were right-skewed and included a large number of birds not associated (with SRI of zero) and birds with very weak associations (SRI close to zero). However, maximum associations strengths were as high as 0.50 in 2018 and 0.56 in 2019. The mean association strength between individuals observed together on at least one occasion was 0.05 ± 0.04 in 2018 (N = 2457 associating dyads) and 0.06 ± 0.05 in 2019 (N = 1038 associating dyads).

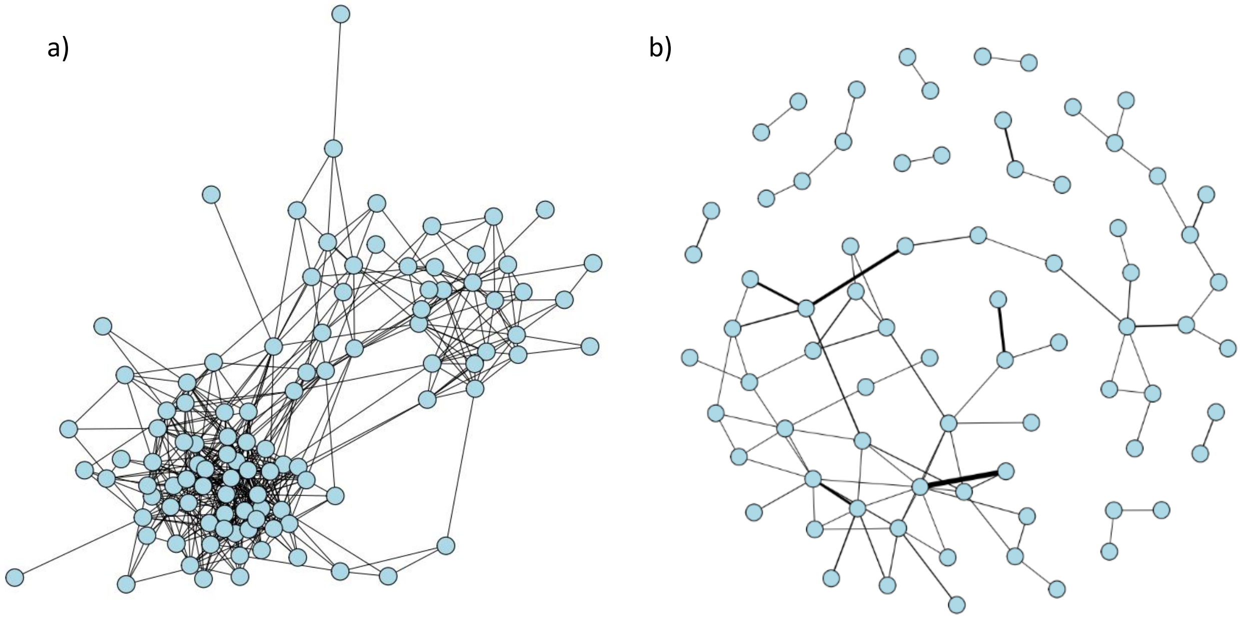

Figure 6.1. Example networks using the full dataset from 2018. (a) Edges with association strengths (SRI) ≥ 0.07 (an arbitrary cut-off) shown with isolated individuals excluded and (b) edges with association strengths (SRI) ≥ 0.13 (an arbitrary cut-off) shown, edges weighted by SRI, and isolated individuals excluded.

6.4.2 Effects of relatedness and inter-nest distances

Inter-nest distances ranged from 0 m (for birds nesting in the same tree) to 744 m (mean 205 m ± 153 SD) in 2018 and from 0 m to 745 m (mean 214 m ± 157 SD) in 2019. Mean pairwise coefficient of relatedness (r_{QG}) for dyads was -0.005 ± 0.167 (range: -0.478 to 0.718) in 2018 and 0.00 ± 0.163 (range: -0.542 to 0.903) in 2019.

In both years, inter-nest distance was related to the strength of the social association between individuals (Figure 6.2a, c), with birds nesting closer to each other having stronger social associations when they were away from the nest (2018: posterior mean = -0.752, 95% credible intervals (CI) = -0.792 to -0.712; 2019: posterior mean = -1.492, 95% CI = -1.572 to -1.412). Relatedness had a negligible effect on the strength of association between individuals (Figure 6.2b, d) with credible intervals overlapping 0 in both years (2018: posterior mean = 0.023, 95% CI = -0.008 to 0.054; 2019: posterior mean = 0.040, 95% CI = -0.002 to 0.083).

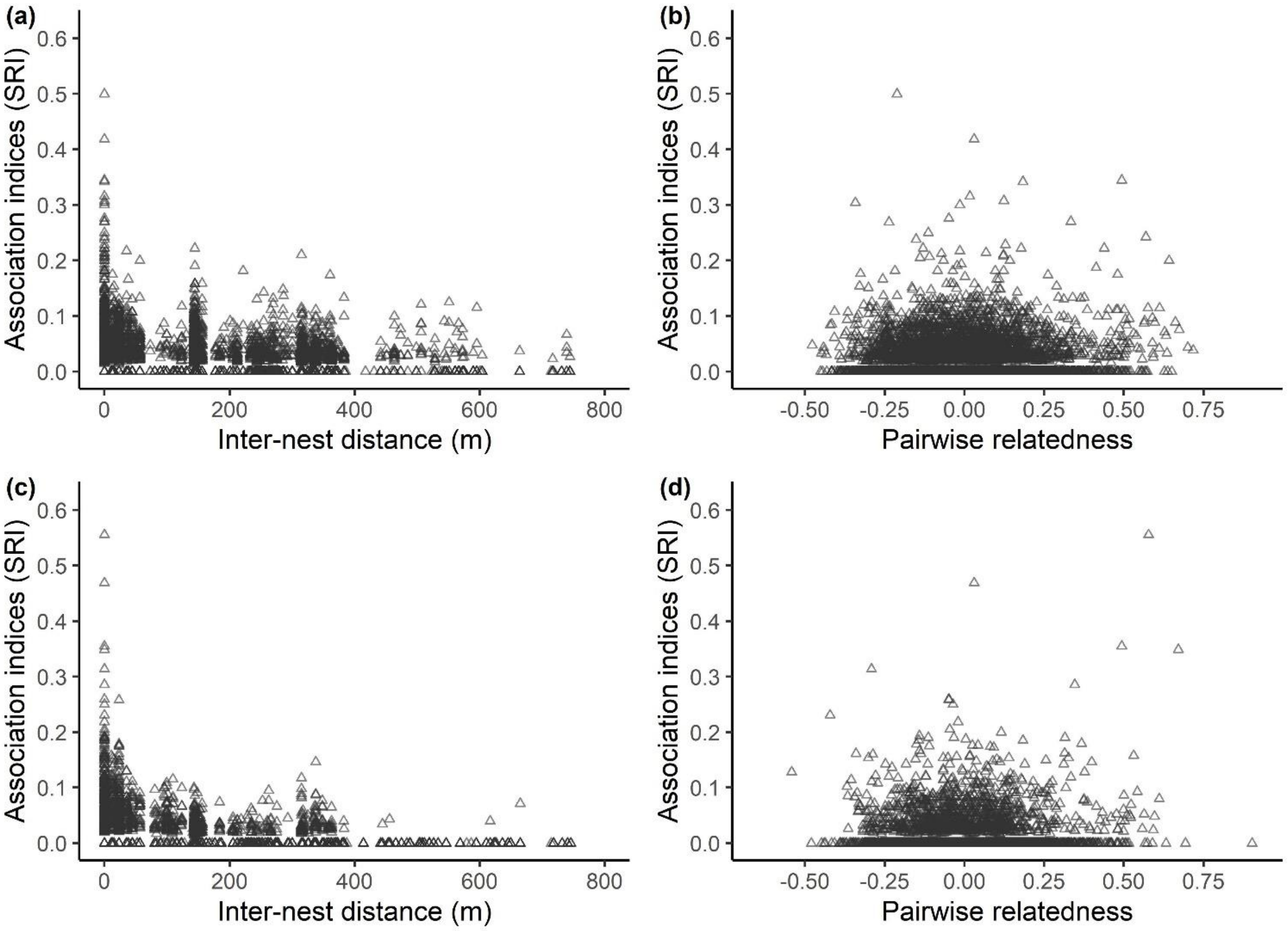

Figure 6.2. The relationship between social association indices (SRI) and inter-nest distances (a, c), and pairwise relatedness (b, d). Number of individuals as follows: 110 individuals in 2018 (a, b) and 82 individuals in 2019 (c, d). Including data collected at a baited food trap.

We found qualitatively the same results when data from the trap was excluded (Figure S6.3); inter-nest distance (2018: posterior mean = -1.151, 95% CI = -1.225 to -1.080; 2019: posterior mean = -1.394, 95% CI = -1.473 to -1.320), but not pairwise relatedness (2018: posterior mean = 0.024, 95% CI = -0.023 to 0.070; 2019: posterior mean = 0.036, 95% CI = -0.008 to 0.079) influenced the strength of the observed associations in both years.

As kin are clustered within nesting trees in the monk parakeet (Dawson Pell et al. 2021), we additionally sought to check whether the pattern of negligible influence of pairwise relatedness on social association strength held when examining only the social associations between birds nesting within the same tree (for model details see Supplementary Material S6.4). We found the same pattern as that revealed by the full data set, with relatedness having negligible impact on the strength of social associations away from the nest (posterior mean = -0.034, 95% CI = -0.098 to 0.029).

6.4.3 Same-sex and opposite-sex associations

When examining same and opposite-sex associations, we found qualitatively similar patterns; increasing inter-nest distance decreases social association strength in female-female (posterior mean = -0.523, 95% CI = -0.653 to -0.397), male-male (posterior mean = -0.793, 95% CI = -0.849 to -0.736), and opposite-sex social associations (posterior mean = -0.747, 95% CI = -0.808 to -0.686), while pairwise relatedness had a negligible effect in all cases (female: posterior mean = 0.003, 95% CI = -0.109 to 0.112; male: posterior mean = 0.025, 95% CI = -0.018 to 0.068; opposite-sex: posterior mean = 0.031, 95% CI = -0.015 to 0.078).

6.4.4 Associations between social pairs and breeding group members

We had data from 28 social pairs available (2018: 16 pairs, 2019: 12 pairs) for our investigation. For 15 pairs both individuals were each other's closest associate (the individual with the highest association strength). Within seven of the remaining pairs, one individual's closest associate was their social mate whereas for the other member of the pair their social mate ranged from second closest associate to 18th. This results in 37/56 (66%) possible associations being closest for the social pair and indicates that social pairs were often each other's closest social associates away from the nest. However, this was not always the case and monk parakeets do consistently associate with other individuals beyond their social pair. Overall, 51/56 (91%) associations between social pairs were within the top 10 closest associates (Figure 6.3a). Only one pair was not observed together away from the nest despite the birds being observed with 49 and 28 other individuals respectively.

Data were available for nine separate breeding groups containing 32 individuals and consisting of 3-5 individuals per group (mean = 3.6) in which all members of the group were also included in our social network. In 23/86 (27%) possible associations, the group member's closest social associate was another member of the same breeding group, with 58/86 (67%) being in each other's top 10 closest associates (Figure 6.3b). These results indicate that members of breeding groups are often close social associates when they are away from the nest, but relationships with group members have lower precedence than social relationships between social pairs.

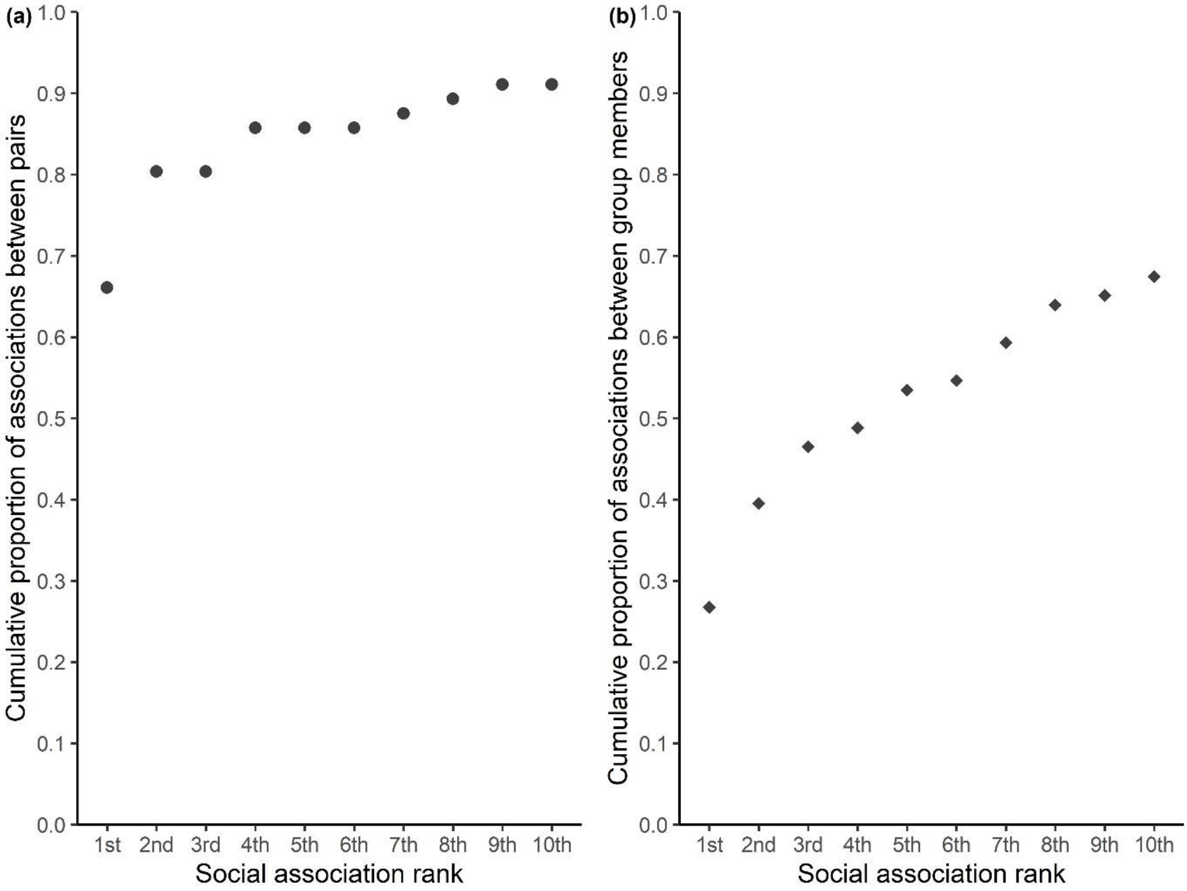

Figure 6.3. Social association ranks (ranked 1^{st} (closest associate) to 10^{th}) between members of a) social pairs (N = 28 pairs, 56 possible social association ranks) and b) group members (N = 32 individuals, 86 possible social association ranks). Shown as a cumulative proportion of the total possible associations.

6.5 Discussion

We used detailed field observations combined with molecular genetic techniques to investigate the influence of inter-nest distance and pairwise genetic relatedness on social associations in free-living monk parakeets. Overall, we showed that social associations away from the nest are generally weak in the monk parakeet, with small numbers of stronger associations. Birds that nested closer together were more strongly associated when away from the nest, however, pairwise relatedness was not associated with social associations despite the role of kinship in determining nest locations in this species (Dawson Pell et al., 2021). These results were qualitatively similar in both years of the study, when we repeated analyses without the data collected at the artificial food source, and when we conducted the analyses on same-sex and opposite-sex associations separately.

Inter-nest distance was negatively associated with social association strength when monk parakeets were away from the nest. This could result from shared space use, familiarity with birds nesting in close proximity, or both. Our result echoes that found in the eastern grey kangaroo, in which space use is more strongly correlated with association strength than kinship (Best et al., 2014). There may be multiple fitness benefits of associating with familiar individuals including: foraging benefits both through reduced kleptoparasitic prey competition (Webster & Hart, 2007) and through locating food patches quicker (Ward & Hart, 2005), enhanced predator avoidance (Griffiths et al., 2004), more stable dominance hierarchies (Höjesjö, Johnsson, Petersson, & Järvi, 1998), facilitation of social learning (Swaney, Kendal, Capon, Brown, & Laland, 2001; Guillette, Scott, & Healy, 2016) and reducing reproductive competition and increasing reproductive coordination or output (Kohn, 2017; Riehl & Strong, 2018). Our result that inter-nest distance is associated with social ties is unlikely to be entirely driven by space use in monk parakeets as the species is non-territorial and individuals are routinely recorded travelling distances for foraging that were beyond the inter-nest distances included in this study. The mean inter-nest distance in this study was approximately 200 m, and previous estimates have indicated that adult monk parakeets regularly travel several hundred meters to forage and have home ranges of 300-400 m (Carrillo-Ortiz, 2009). In addition, recently fledged juvenile monk parakeets have been recorded up to 1500 m away from their nests, although distances of up to 500 m were more common (Chapter 4). This means that despite the extensive overlap of home ranges at our study site of 30 ha, individuals still preferentially associated with familiar individuals.

In contrast, we found no significant influence of genetic relatedness on the strength of social associations away from the nest in the monk parakeet. This result is particularly interesting in light of the fact that relatives are clustered together in both compound nests and nesting trees (Dawson Pell et al., 2021) and yet these nesting associations with kin did not extend to movements away from the nest. Our finding that genetic relatedness does not predict social associations when foraging echoes similar findings in the blacktip reef shark, *Carcharhinus melanopterus* (Mourier & Planes, 2021), the common racoon, *Procyon lotor* (Hirsch et al., 2013), and wintering populations of the golden-crowned sparrows, *Zonotrichia atricapilla* (Arnberg, Shizuka, Chaine, & Lyon, 2015). But it contrasts with many other species in which kinship does play a key role in shaping social associations, for instance in common eiders, *Somateria mollisima* (McKinnon et al., 2006), African elephants, *Loxodonta africana* (Chiyo et al., 2011), and Australian bottlenose dolphins, (Diaz-Aguirre et al., 2019). The negligible influence of relatedness on social associations away from the nest may be the result of social pairs associating together away from the nest, as indicated by our results showing that in 66% of cases the closest social associate of an individual was their social mate. No inbreeding has been detected overall at our study site (Dawson Pell et al., 2021) and pair relatedness is typically low (Chapter 5). However, pairs are not always the strongest social associates and other social associations exist in monk parakeets that can be stronger than that of the pair. Notably, this study was conducted in the breeding season, during which the females spend extended periods of time incubating eggs in the nest. Therefore, pairs may be observed separately more often during this period and a different pattern may be observed if this study was repeated during the non-breeding season. Members of breeding groups were also often close social associates when away from the shared nest, however, group members were amongst each other’s closest associates less frequently than social pairs (91% pairs, 67% breeding group members within the top 10 closest associates).

Studies of parrot social structure in the wild are limited, likely due to the technical challenges of making observations of a largely canopy dwelling taxon often with high mobility, that are notoriously challenging to mark successfully (e.g. Meyers, 1994). Our study therefore adds to the limited but growing number of studies investigating patterns of social associations in the Psittacidae, a family often discussed in the context of social evolution and complexity (e.g. Emery, 2006; Hobson et al., 2014). As with many parrot species (e.g. Buhrman-Deever, Hobson, & Hobson, 2008), monk parakeets exhibit fission-fusion dynamics (Hobson et al., 2014); we did not address changes in flock composition directly in this study, instead we used the 'gambit of the group' method to assess social ties. Despite this fission-fusion social system that can mask the presence of social associations, we found monk parakeets had some strong social ties with others away from the nest. Stable social relationships have been shown to be present in another parrot species adapted to living in the urban environment, the sulphur-crested cockatoo, *Cacatua galerita*, that also has a fission-fusion social system (Aplin, Major, Davis, & Martin, 2020). In the sulphur-crested cockatoo it is mainly roost-site choice that drives social associations (Aplin et al., 2020), a pattern similar to that revealed here.

The mechanism through which social associations are maintained in the monk parakeet is unknown. However, monk parakeets have individual vocal signatures (Smith-Vidaurre et al., 2020) which could facilitate social interactions with familiar individuals away from the nest through mechanisms of social learning. Indeed, studies on captive populations indicate that monk parakeets may be able to discriminate social associates through contact calls (Hobson, John, Mcintosh, Avery, & Wright, 2015). However, unlike other parrot species that have been shown to produce contact calls that are specific to certain roost sites (e.g. Wright, 1996; for a review of vocal dialects in parrots see Wright & Dahlin, 2017), there has been no evidence of 'higher-level' vocal signatures beyond the level of the individual in the monk parakeet, such as at the level of the nest-site (Smith-Vidaurre et al., 2020), that could facilitate associations between groups of individuals that share a nesting tree when they are away from the nest.

We did not assess long-term associations in this study, however, as a relatively long-lived species, the monk parakeet may have long-lasting associations that may have fitness implications (Silk et al., 2009). Indeed, monk parakeets at our study site demonstrate high site fidelity, which may facilitate long-term social associations between individuals (Dawson Pell et al., 2021). An investigation into whether monk parakeets have long-term associations may be fruitful in terms of understanding social dynamics in long-lived species but also in terms of the potential fitness implications of social bonds in this species. The function of social associations may also differ between pairs and breeding groups with possible links to reproductive roles, prospecting behaviour and mate choice; these possibilities warrant further investigation.

For all of our analyses, we observed fewer females than males and in most cases males were observed significantly more than females. This is likely due to the fact that females incubate the eggs for long periods during the breeding season and are therefore less likely to be observed away from the nest (Eberhard, 1998; Fatsy 2008). Males also feed incubating females, so females may make fewer foraging trips which reduces their chances of being observed (Eberhard, 1998; Fatsy 2008). An alternative explanation is that females travel further from the nest and were therefore detected less frequently by observers whose efforts were focussed in the core study area, although we think this unlikely due to the high volume of observations in this study and the breeding behaviour of females. If the study was replicated in the non-breeding season we may expect males and females to be observed at a more consistent rate if breeding behaviour indeed influences the probability of observing individuals.

In conclusion, we studied the social structure and the factors underlying social associations in free-living monk parakeets. This system is highly tractable for assessing social associations as flocks are often highly visible and the study population has a large number of uniquely identifiable individuals. We demonstrated that social associations of monk parakeets away from the nest are relatively weak, with some stronger connections between individuals detected. The strength of social associations is driven by inter-nest distance rather than kinship. This result may be explained by preferential association with familiar individuals, perhaps in combination with shared space use. Finally, our results have implications for the understanding of the drivers of social associations in free-living animals and adds to the limited knowledge of parrot social structure.

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6.6 Supplementary information for:

Social associations are predicted by nest proximity, but not kinship in a free-living social parrot

S1. Survey locations

Parks and streets surveyed: Passeig de Lluís Companys, Plaça de Tetuan, Avinguda Diagonal, Rambla del Raval, Carrer de Marina, Parc de Carles I, Parc de l'Estació del nord, Jardins del Bosquet dels Encants, Plaça de Pablo Neruda, Plaça del Duc de Medinaceli, Parc de la Nova Icària, Plaça de Pau Vila, Parc de la Barceloneta.

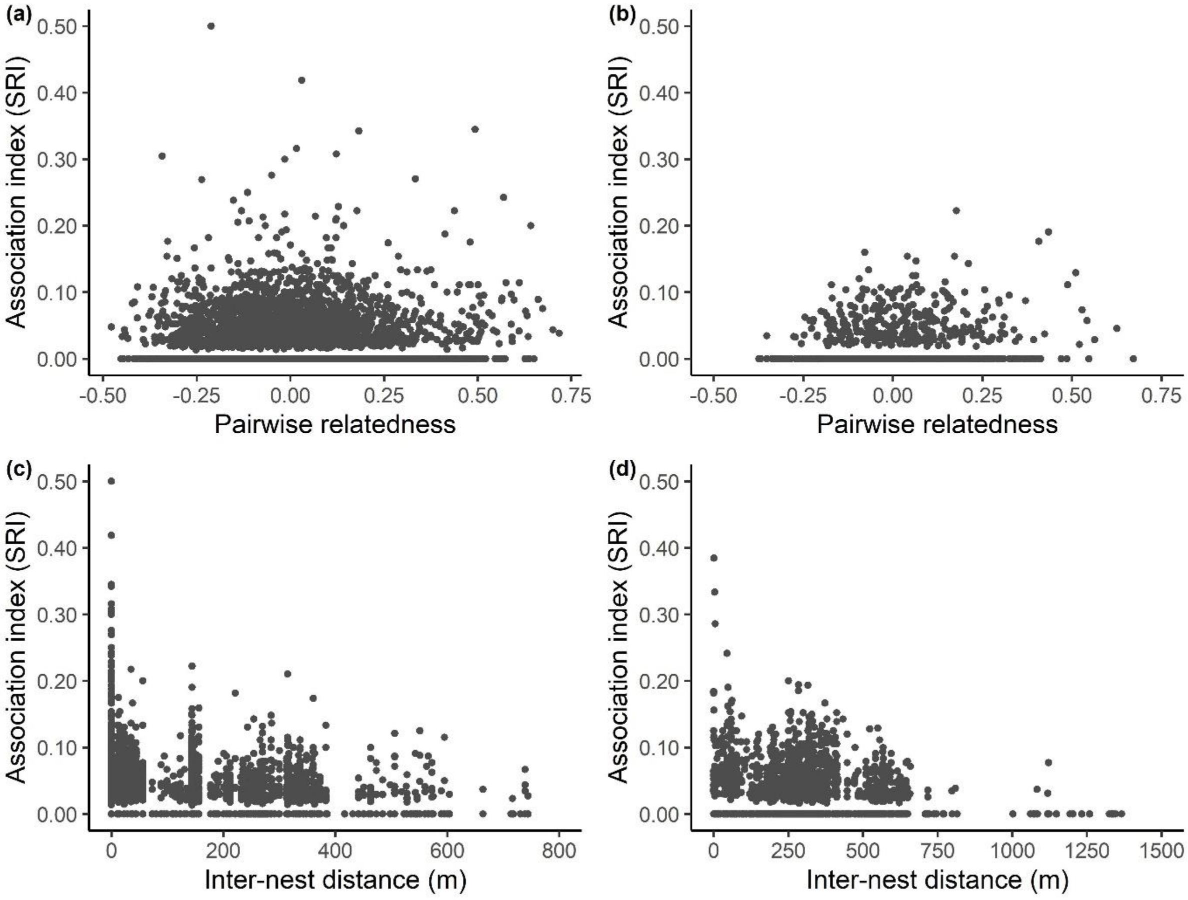

Figure S6.1. The relationship between social association indices (SRI) and pairwise relatedness (a, b), and inter-nest distances (c, d) for visual assessment of bias in the dyads removed for having missing data. Datasets shown as follows: (a) all dyads of birds with complete data; (b) dyads excluded from the main dataset for having no inter-nest distance data available (c) all dyads with a full dataset and (d) dyads excluded from the main dataset as they had no relatedness data available.

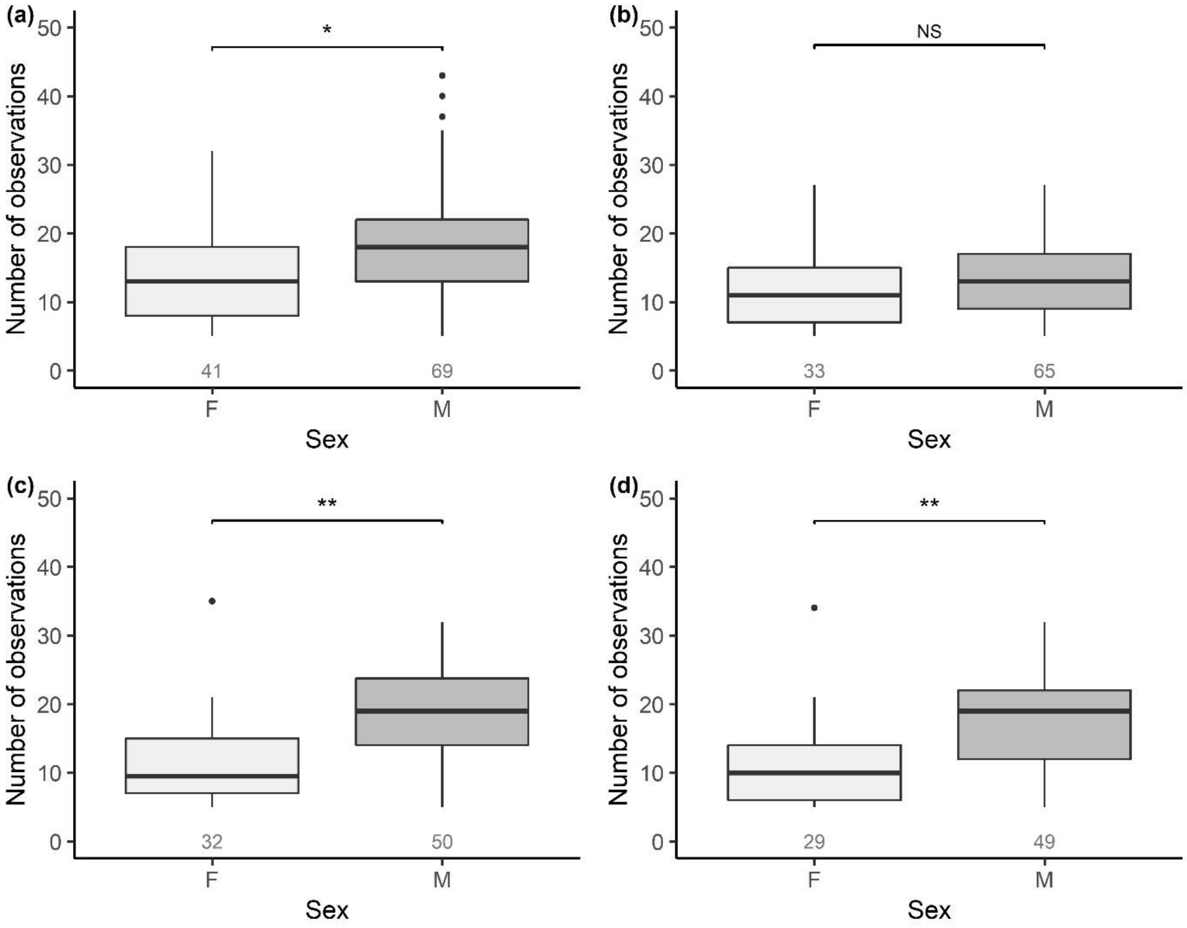

Figure S6.2. The number of observations of males and females in (a) 2018 including trap data, N =110, (b) 2018 excluding trap data N = 98, (c) 2019 including trap data N = 82 and (d) 2019 excluding trap data N = 78. Boxplots indicate the interquartile range (box upper and lower limits), median (thick lines within boxes), maximum values excluding outliers (lines extending from boxes) and outliers (filled dots). Sample sizes are given above the x-axis for each sex. NS = non-significant, *p < .01, **p < .001.

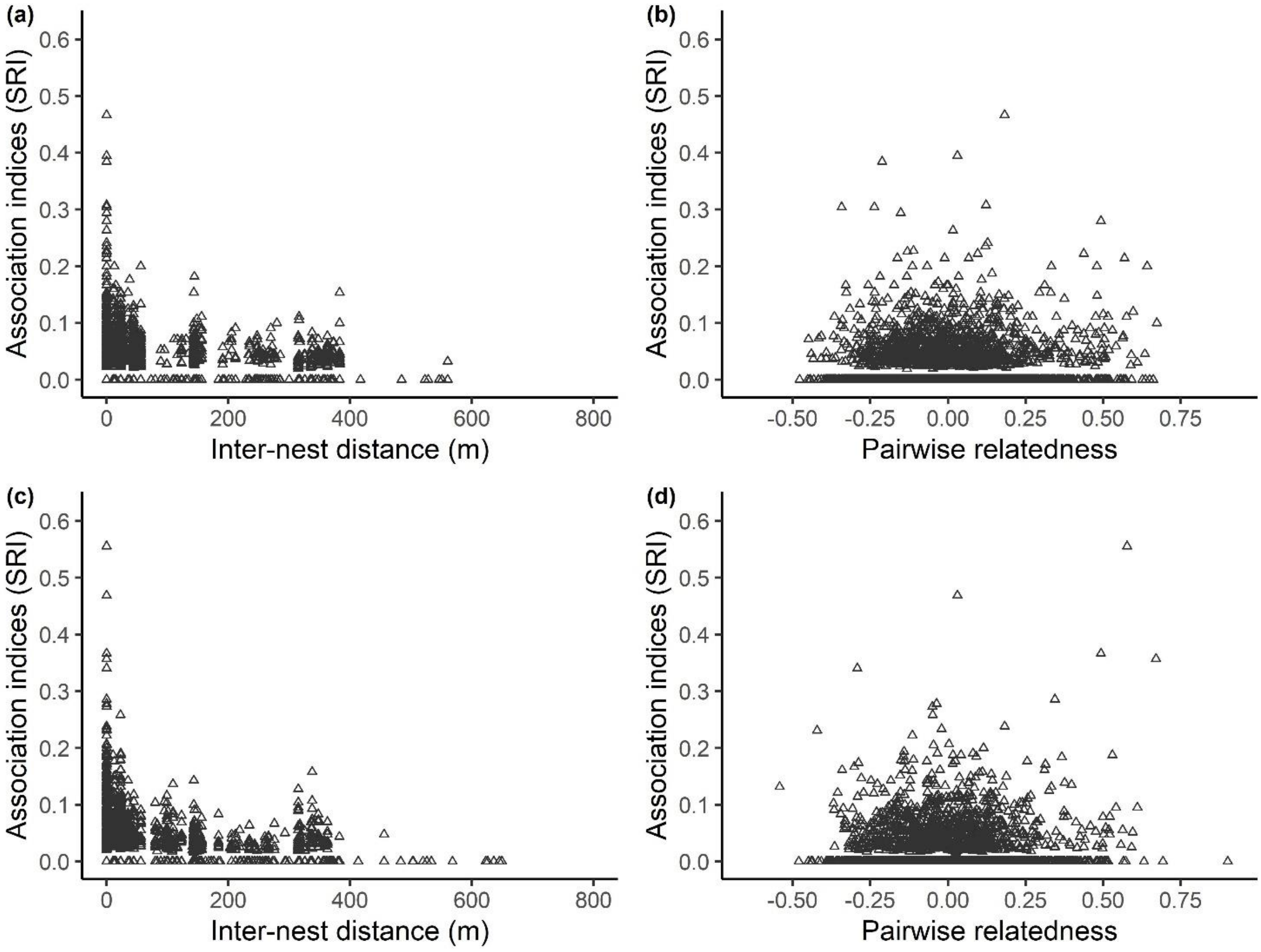

Figure S6.3. The relationship between social association indices (SRI) and inter-nest distances (a, c), and pairwise relatedness (b, d) when data collected at an artificial food source was excluded. Number of individuals as follows: 98 individuals in 2018 (a, b) and 78 individuals in 2019 (c, d).

S6.4 Social association strength and relatedness within nesting trees

We ran an additional model to examine any association between pairwise relatedness and social association strength for birds nesting within the same tree only. Using the larger 2018 dataset, including data collected at the artificial food trap we had data from 702 dyads. As with the models previously described, we fitted Bayesian multi-membership regression models in Stan (Stan Development Team 2020a) via RStan (Stan Development Team 2020b) using the brms package (Bürkner, 2017). For this model, we used a binomial likelihood with association strength (SRI) as the response, and our predictor variable was pairwise genetic relatedness transformed to a z score. Our model was fitted over 4 independent chains with a warmup of 3000 followed by 6000 iterations of sampling and we applied weakly regularizing priors in this model.

7. General Discussion

7.1 Research summary

In this thesis, I have addressed questions pertinent to both fundamental and applied ecology through investigations into the social and genetic structure of a population of the invasive parakeet species, the monk parakeet, *Myiopsitta monachus*. In brief, I have combined detailed field observations with molecular genetic techniques to reveal patterns of fine-scale genetic structure driven by specific demographic processes, investigated factors affecting nesting habitat selection, characterised the breeding system, investigated cooperation and conflict at the nest, and examined patterns of social associations. Below I provide a summary of the main findings presented in each chapter.

In chapter 2, I developed new microsatellite markers for monk parakeets and tested their cross-species utility in the ring-necked parakeet, *Psittacula krameri*, another widespread invasive species. I also optimised these new markers in multiplexes. In this chapter, I tested nine sex-markers and found a number of markers that can be used to successfully sex individuals of both species. Z chromosome polymorphisms were revealed in the ring-necked parakeet when using two of the sexing markers. These microsatellites enabled the genetic analyses throughout my thesis and will be useful to other researchers studying both monk parakeets and ring-necked parakeets. They may also be useful for other species; monk parakeets and ring-necked parakeets are not closely related within the parrot family and, as some of the markers worked in both species it is likely that some of them will work in other parrot species too.

In chapter 3, I investigated patterns of fine-scale genetic structure at a range of spatial scales and linked the observed patterns to specific demographic processes in the monk parakeet. I revealed significant fine-scale genetic structure at the level of the nesting tree for both sexes and at the level of the compound nest for males. There was no significant population genetic structure beyond the nesting tree, at least over the distance of 400 m investigated in this study. These patterns were driven by natal philopatry, limited natal dispersal distances and the coordinated dispersal and nesting of sibling coalitions combined with high adult site fidelity. Thus, monk parakeets can be characterised as living in ‘kin neighbourhoods’, creating a likelihood of social interactions with relatives. These findings have implications for various social behaviours, including colony formation and kin-selected cooperation, but also potential costs through inbreeding and kin competition. More generally, this chapter contributes to our understanding of how multiple demographic mechanisms can lead to kin-structured populations in nature.

In chapter 4, I investigated the dispersal behaviour and, specifically, the choice of nesting trees by natal dispersers. Recently fledged juveniles exhibited extensive ranging movements in the first four months post-fledging; this ranging behaviour was unrelated to eventual dispersal decisions or sex. I then examined evidence for natal habitat preference induction in the monk parakeet, demonstrating a preference for nesting trees of the same type as the natal tree type for one nesting substrate. I also provided evidence for the maintenance of habitat preference following breeding dispersal by adult birds. Finally, I showed that conspecific breeding success was unlikely to provide a useful source of public information regarding the suitability of nesting substrates at our study site. These results have implications for patterns of dispersal in this worldwide invasive species and may also influence management decisions by helping to predict range expansions, particularly at fine spatial scales. In addition, this chapter contributes to our understanding of the process of habitat selection in nature, the results of which can have profound ecological and evolutionary consequences.

In chapter 5, I explored monk parakeet behaviour at the nest, with a particular focus on their social system, cooperative behaviours and areas of conflict. I first characterised the breeding system and showed that monk parakeets breed in pairs most of the time but that approximately 20% of breeding attempts are by breeding groups. There was marked diversity in group composition and genetic relatedness among group members, revealing the complex nature of group formation in this species. I also examined nest building and maintenance behaviours and showed that males engage in these behaviours significantly more than females. I also provided evidence of frequent kleptoparasitism of nest material, which may represent a cost of colonial nesting in this species. Multi-female groups tended to produce larger clutches, implying that co-breeding occurred in such groups but overall, there was no significant difference between pairs and groups in either clutch size or the number of fledglings. Parentage analyses and examinations of within-brood relatedness revealed extra-pair paternity in approximately a quarter of broods attended by social pairs, and shared parentage within breeding groups, with some evidence of possible non-breeding helpers. Thus, the breeding system in monk parakeets precludes simple definition, but the flexibility revealed in this chapter may be important for research into the evolutionary origins of cooperative behaviour.

In chapter 6, I examined social associations in monk parakeets when birds were away from the nest, describing the strength of associations and the correlates of observed social ties. Overall, associations are relatively weak between individuals when away from the nest. The strength of social associations was related to inter-nest distance, but not pairwise genetic relatedness. This pattern held when we removed data collected at a large artificial food source and when we looked at same-sex and opposite-sex associations separately. I also examined whether pair members were each other's closest social associates when away from the nest and showed that in most cases, an individual's closest associate was their social mate, although individuals also have social bonds outside of the pair. Members of breeding groups were often close associates too, but were amongst each other's closest associates less frequently than pairs. Studies of parrot social structure are few, probably due to the intractability of most species for detailed observations, therefore this work adds to our understanding of social behaviour in the Psittacidae and to our understanding of the drivers of social associations in nature.

7.2 Implications and future directions

7.2.1 Living with relatives and kin recognition

We revealed significant genetic structure at a range of spatial scales in the monk parakeet, driven by several demographic processes including both natal and breeding dispersal behaviour. These characteristic demographic mechanisms lead to the formation of 'kin neighbourhoods' in the monk parakeet with subsequent increases in opportunities for kin selection to operate (Hamilton, 1964) as well as the risk of kin competition (West et al., 2002) and inbreeding (Pusey & Wolf, 1996; Keller & Waller, 2002). Despite living in close proximity with relatives of the opposite sex, we detected no indication of significant inbreeding at the level of the population, and few pairs had relatedness levels above that expected for unrelated individuals. When relatedness within groups is variable or when a species lives in 'kin neighbourhoods', mechanisms of kin discrimination that enable individuals to avoid inbreeding or direct aid towards relatives may be selected for (Cornwallis et al., 2009). Our findings regarding the population genetic structure of the monk parakeet suggests that a mechanism of kin recognition acts to reduce the risk of inbreeding; such a process of recognition could act in concert with sex-biased dispersal, a passive mechanism for inbreeding avoidance. To address whether there is active avoidance of related individuals as mates, a comparison could be made between observed mate choice and simulated distributions generated from models of random mate choice (e.g. Szulkin, Zelazowski, Nicholson, & Sheldon, 2009; Leedale et al., 2020a).

In addition to the increased risk of inbreeding as a result of living in close proximity to relatives, there is also likely to be a degree of kin competition in the monk parakeet. Kleptoparasitism of nest material is potentially quite costly for monk parakeets as approximately a quarter of all material was overtly stolen at our study site, indicating that kleptoparasites may cause a significant burden in terms of nest maintenance. Nest building is an energetically expensive activity (Mainwaring & Hartley, 2013), and monk parakeet nests are maintained year-round and can also be very large (a single two-chambered nest at our study site contained approximately 10,000 sticks with an estimated weight of 100 kg, J.C. Senar unpublished data), so theft of material may represent a significant energetic cost. As relatives are found nesting in the same trees, and 90-98% of observed thefts happened between nests within the same tree, there is likely to be conflict between kin over nest material. It may be interesting to examine nest material kleptoparasitism in relation to genetic relatedness between nest occupants to investigate whether individuals steal indiscriminately or tend to avoid nests of kin.

Living near related individuals can have fitness benefits, for example by reducing both permanent somatic damage and current energetic costs (Bebbington et al., 2017), increasing juvenile recruitment (Lee, Jang, Dawson, Burke, & Hatchwell, 2009) and survival (Brown & Brown, 1993), and increasing reproductive success (Fowler, 2005). Having demonstrated in this work that relatives cluster at a variety of spatial scales in the monk parakeet, there are opportunities in this system to examine in depth the costs and benefits of living and breeding near kin. Specifically in the case of the monk parakeet, it may be interesting to investigate whether kinship limits social conflict within nests and nesting trees through reduced frequency of physical fights between relatives (e.g. Bebbington et al., 2017), or whether reproductive success within compound nests or nesting trees may be influenced by kinship with neighbouring breeders (e.g. Fowler, 2005).

Identifying possible mechanisms of kin recognition in the monk parakeet would improve our understanding of how the risks of inbreeding and kin competition in kin-structured populations are mitigated. A potential mechanism of kin recognition could involve using individual vocal signatures; such signatures have been detected in the contact calls of monk parakeets in its native range (Smith-Vidaurre et al., 2020), and playback experiments revealed monk parakeets may use contact calls to identify social partners in captivity (Hobson, John, McIntosh, Avery, & Wright, 2015). However, whether individual vocal signatures or shared group call structure, or both in combination, are used to identify kin remains to be determined. Investigations into whether call similarity correlates with kinship would therefore be worthwhile and would add to our understanding of monk parakeet social structure, breeding decisions and associations. Call similarity is positively correlated with kinship in the long-tailed tit, *Aegithalos caudatus*, (Sharp, McGowan, Wood, & Hatchwell, 2005; Leedale, Lachlan, Robinson, & Hatchwell, 2020) and a few other cooperative breeders (e.g. Price, 1998;

McDonald & Wright, 2011), and if that is also the case in the monk parakeet it may help to prevent inbreeding and avoid competition.

7.2.2 Cooperation and breeding behaviour

There has been recent renewed interest in the use of social network analysis in the investigation of the evolution of cooperative behaviour and how social structure may influence the spread and maintenance of cooperative behaviour (for review see Gokcekus, Cole, Sheldon, & Firth, 2021). For instance, individuals with stronger social connections may be more likely to cooperate, as seen in guppies, *Poecilia reticulata* (Croft et al., 2006). Such investigations may be addressed well in a study system like that of the monk parakeet. For instance, it could be of interest to explore if those individuals with strong social connections away from the nest site cooperate in building compound nest structures, form breeding groups in the breeding season, or jointly chase nest material kleptoparasites from nests.

It remains an open question as to whether the compound nests of monk parakeets are an emergent property of pairs or groups investing in their own nest chamber, or structures built and maintained through cooperative investment. In sociable weavers, *Philetairus socius*, another species that builds large communal nest structures, cooperative investment in the communal component of the nest structure is kin-directed (van Dijk et al., 2014). We found that at least for males, relatedness is higher than expected within compound nest structures, which may indicate that investment in the compound nest structure as a whole may benefit kin in the monk parakeet. Indeed, the idea that individuals may cooperate in building compound nests in the monk parakeet is supported by the fact that builders regularly delivered sticks to locations all over the nest structure, including areas not immediately adjacent to their own nest chamber (F.S.E.D.P. personal observation). Compound nests can reach enormous proportions, so building and maintenance behaviours may be important for nest structural integrity hence may drive investment in the compound nest as a whole. On the other hand, unlike sociable weavers (van Dijk et al. 2014), there is no clear spatial distinction between cooperative and selfish nest-building in monk parakeets, or at least not in the relatively small compound nests observed in Barcelona. However, individuals attempting to build new chambers on existing nests were often not tolerated at our study site, with frequent physical fights and vocalisations between the resident birds and the individuals attempting to join their nest (F.S.E.D.P. personal observation). This indicates there is conflict over compound nest building and birds are initially territorial over their nest structure when newcomers arrive. It would be interesting to assess the level of tolerance for newcomers to the nest based on kinship in the monk parakeet.

There are many parrot species for which the breeding system is either assumed or unknown (Cockburn, 2006). In this work we have presented evidence of a diverse and flexible breeding system in the monk parakeet and have added to our understanding of the broad range of breeding systems within the Psittacidae. There are many avenues for future research in the monk parakeet in terms of the breeding system. For instance, the drivers behind cooperation within breeding groups may vary based on the route to group formation and group composition may influence patterns of, for instance, extra-pair reproduction (e.g. Hajduk, Cockburn, Osmond, & Kruuk, 2021). Investigations into the share of parentage within breeding groups formed through different routes could also be of interest in terms of our understanding of selection for cooperation in this species but also the evolution of cooperative behaviour. Stemming from investigations into the share of parentage, there are also questions regarding investment by group members in the breeding attempt in relation to their share of parentage. We compared clutch sizes and the number of fledglings between pairs and breeding groups and found no significant differences (Chapter 5), however, we were not able to assess fledgling quality (te Marvelde, McDonald, Kazem, & Wright, 2009; Bolopo, Lowney, & Thomson, 2019), or juvenile survival (Hodge, 2005) or other potential long-term impacts of being raised by a group compared to a pair; all such investigations could be fruitful in future. In summary, the system addressed in this thesis presents many opportunities for future research into cooperative behaviour and flexible breeding systems.

Our study also highlights the importance of studying different populations of the same species to build a more detailed picture of the behaviour of a species and to examine flexibility in behaviour. For instance, it has been previously shown that the reproductive capacity of monk parakeets is higher in their invasive range, with double the fledging success, the percentage of pairs attempting a second brood within the breeding season being three times higher and 55% of one-year-old birds breeding compared to none in the native range (Senar et al., 2019). Information of this nature is vital for population modelling and in the case of the monk parakeet, for accurate modelling of population growth and the potential spread as an invasive species. In this thesis, we also indicated there may be differences between the native and invasive range in terms of patterns of extra-pair paternity (EPP), showing lower levels of EPP at our study site than those reported in some areas of the native range (Martínez et al., 2013) and also contrasting with the reports of sexual monogamy reported for both an invasive and native population (Gonçalves da Silva et al., 2010). Such differences between populations are perhaps not unusual (e.g. Indykiewicz, Podlaszczuk, & Minias, 2017) and collecting data from multiple populations or areas can add to our understanding of the ecological pressures selecting for such variable behaviours.

7.2.3 Dispersal, habitat selection and ranging behaviour

This study has shown that natal dispersal is female-biased and that both natal and breeding dispersal distances are limited in the urban environment, with natal dispersal distances often shorter than observed ranging distances. I also presented evidence of coordinated nesting and dispersal of sibling coalitions. This work adds to the growing number of studies showing that associations between relatives can be maintained after natal dispersal (e.g. Lee, Lee, & Hatchwell, 2010; Williams & Rabenold, 2005; Ridley, 2012). These coalitions were relatively easily detected in monk parakeets as siblings shared nesting chambers, even following dispersal. However, that may not always be the case. For example, dispersal of sibling coalitions in the long-tailed tit, involves relatives dispersing in similar directions and distances, although not attending the same nest, at least for the first nesting attempt of the season (Sharp, Simeoni, & Hatchwell, 2008). These coordinated dispersal movements by related individuals that are subtler may be more challenging to detect in the field without studying marked individuals over multiple seasons or applying detailed genetic investigations. However, a better understanding of the prevalence of coordinated dispersal of relatives would add to our understanding of dispersal ecology in general and our understanding of the potential for interactions with kin post-dispersal.

Dispersal decisions were also influenced by natal habitat preference induction (NHPI), a phenomenon rarely demonstrated outside a laboratory environment. Therefore, this work adds to the growing evidence of the impact of the natal environment on habitat choice and is important in our general understanding of the process of habitat selection. It could be fruitful to investigate whether preferences stemming from the natal environment persist over time in nature. One study has attempted to investigate whether the effects of NHPI wane over time, and showed that NHPI seems to weaken when common loons, *Gavia immer*, settle on their second territories (Piper et al., 2013), although this result was tentative and investigations of this nature are rare. Using a long-term dataset, it would also be interesting to disentangle the importance of the natal experience compared with for instance, personal breeding experience or the reproductive success of conspecifics in habitat selection decisions throughout life. Such investigations could shed light on the lifetime fitness consequences of the natal experience shaping habitat selection.

In the case of the monk parakeet, examining patterns of habitat selection could help with its management as an invasive species. Nesting substrates vary between locations in the monk parakeet, but within each location certain substrates are used consistently despite the availability of alternatives. For example, cedars, *Cedrus spp*, are preferred in both Madrid (Roviralta & Garc, 2001) and Rome (Di Santo et al., 2017) despite other suitable substrates being available. A test of whether targeted management of preferred nesting substrates helps to control the species could be worthwhile for this worldwide invasive species.

Habitat exploration and ranging behaviour by pre-dispersal juveniles is also an understudied area of dispersal ecology with many potential avenues of research to explore further. The vast majority of studies report dispersal outcomes only, with pre-dispersal exploratory forays and ranging behaviour being studied in detail only a handful of species (e.g. Haughland & Larsen, 2004; Cox & Kesler, 2012; Debeffe et al., 2013). Such forays can influence the direction and distance of dispersal (Haughland & Larsen, 2004b), be indicative of dispersal syndrome (disperser or philopatric; Debeffe et al., 2013) or reflect a sex bias in dispersal behaviour (Fitzpatrick et al., 1999; Sherer, Fish, & Service, 2020; Woolfenden & Fitzpatrick, 1984). This thesis adds to the limited number of studies examining pre-dispersal movements, however, the possible ecological and evolutionary consequences of such ranging movements and their links to dispersal decisions and behaviour warrant further research attention. Monk parakeets would likely be suitable for the use of animal-borne trackers (‘bio-loggers’) due to their size and high nest-site fidelity. The use of such devices would provide more detailed data on ranging and dispersal behaviour and offer a valuable insight into the movement of these birds, offering particular insight into movement patterns in the urban environment.

7.3 Conclusions

The work presented here has addressed questions pertinent to our understanding of evolution and fundamental and applied ecology and has yielded novel insights into the behavioural and evolutionary ecology of monk parakeets. This thesis has provided evidence regarding several understudied phenomena and has implications for our understanding of dispersal ecology, population genetic structure, breeding systems, cooperative behaviour and invasive species management amongst other topics and has also raised many questions for further study.

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