Conspecific brood parasitism in waterfowl and cues parasites use

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Abstract

Conspecific brood parasitism (CBP) occurs in various insects, fishes and birds, but it is disproportionately common in waterfowl (Anatidae). Studies of CBP in Anatids therefore have helped to develop a fundamental conceptual framework with which to explain this intriguing behaviour. Yom-Tov (1980) first drew attention to CBP, and Andersson and Eriksson (1982) also hinted at the fascinating behavioural, ecological and evolutionary aspects of CBP in waterfowl. Several reviews followed these early papers, but much has been learned more recently about CBP in waterfowl. Here we aim to review the traditional conceptual framework of CBP in waterfowl and to consider empirical studies that have attempted to test related hypotheses. The survey provided support for the hypotheses that CBP allows some females to reproduce when not otherwise possible, whereas other females use parasitic egg-laying as a way to enhance their fecundity. A recently developed framework that considers CBP as part of a flexible life-history strategy could provide a useful direction for future studies of CBP. A second aim of this review is to consider the use of cues by conspecific brood parasites seeking suitable places to lay eggs parasitically. Recent studies have revealed remarkable cognitive abilities in parasitic females, but the actual mechanisms remain unknown. Clearly, breeding females are sensitive to cues such as nest site security, patterns of previous nest use or success, clutch size, and perhaps even the degree of kinship between hosts and other parasites. Indeed, additional investigations of CBP are needed to provide a better understanding of the processes and patterns of this avian reproductive strategy.

Key words: Anseriformes, brood parasitism, information use, life-history, nest predation risk.

Conspecific brood parasitism (CBP) is an alternative reproductive tactic in which a female lays eggs in the nests of other conspecific individuals and leaves the subsequent care of the eggs and young to the host female. CBP has been documented in at least 234 species of birds and is particularly prevalent in Anseriformes where it has been reported in 76 of the 161 species (Yom-Tov 2001).

Several comprehensive reviews have been published on the hypotheses for the occurrence and evolution of CBP in birds (Eadie *et al*. 1988; Rohwer & Freeman 1989; Sayler 1992; Lyon & Eadie 2008) and this paper does not intend to provide another broad-ranging overview of the CBP breeding strategy. However, empirical and theoretical research on CBP has grown since the original paper by Yom-Tov (1980) and much of this work has focused on waterfowl (Fig. 1). Development of theory to explain CBP grew through the 1990s peaking in 2001–2005. Empirical studies
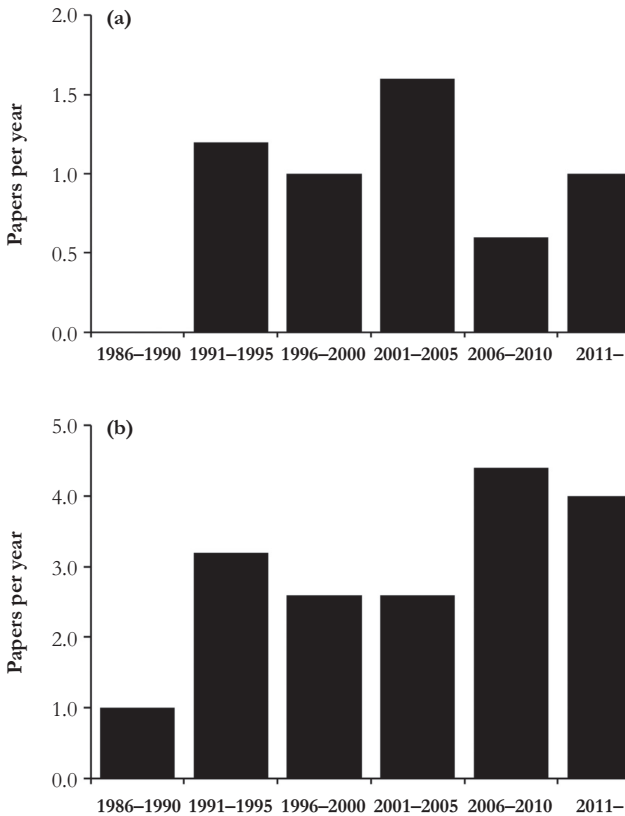

Figure 1. Number of (a) theoretical papers published on CBP in general (top panel; *n* = 24 papers in total), and (b) empirical papers published on CBP in waterfowl (bottom panel; *n* = 77) over the past three decades.

lagged and reached their highest frequency in the last 5–10 years (Fig. 1). Many advances have been made, but there is a surprising amount that is not yet known. Indeed, for many species, it is still not clear which females within a population pursue this behaviour, nor do we fully understand the fitness consequences to parasites or their hosts. Much of the work to date has focussed on ecological factors that correlate with the occurrence of CBP, but longitudinal studies of females are still rare. Similarly, most studies are observational, albeit with an expanded toolkit of molecular genetic techniques which help to ascertain maternity. Experimental studies are uncommon with a few notable exceptions (Eadie 1989; Pöysä 2003a,b; Pöysä *et al.* 2010; Odell & Eadie 2010). Despite these gaps, the field is now at a point where some retrospection would be valuable. The initial goal of this paper therefore is to review briefly the traditional set of hypotheses posed to account for CBP in waterfowl and to evaluate how existing empirical work meets those expectations. We then offer an alternative conceptual framework proposed by Lyon & Eadie (2008) that could advance our understanding of this behaviour more effectively.

Secondly, considerable growth in this field involves the information that might be available to parasites and hosts to modulate their behaviour in an adaptive manner. How do females choose a nest or host to parasitize? What information might be available to females to shape their behavioural decisions? Brood parasites gain fitness by having other females provide parental care for their offspring. Even though parasitism represents a relatively cheap way to gain fitness at the expense of other individuals, this does not mean that parasites should lay their eggs indiscriminately. To the extent that fitness from parasitism can be enhanced by decisions that parasites make regarding where to lay their eggs, or how many eggs to lay in a given nest, natural selection should favour those decisions or tactics. However, parasites must be able to gather useful information about potential host nests that they can use to inform their laying decisions. Do they gather this information, and if so, what cues do they use? A second goal of this paper therefore is to examine the growing body of work that is beginning to explore the cues used by conspecific brood parasites. The focus here is on specific cues that the parasites may use to select host nests into which to lay eggs. This is not meant to imply that cues and decisions used by hosts are not important. For example, hosts may desert nests in response to CBP (Eadie 1989; Jaatinen *et al.* 2009), resulting in the direct loss of parasitic eggs. Hosts could also influence which parasites gain access to their nests (Åhlund 2005).

Conspecific brood parasitism in waterfowl

Here we provide a brief overview of the set of traditional hypotheses that have been suggested to explain CBP, outlined in earlier more comprehensive reviews (including Andersson 1984; Eadie *et al.* 1988; Sayler 1992; Lyon & Eadie 2008), and examine the evidence from the literature in support of

these hypotheses for waterfowl. We then present a revision of the framework of hypotheses proposed by Lyon and Eadie (2008) to help guide further research in this field.

Is it parasitism or inadvertent competition?

Some early researchers considered parasitic egg-laying (also called "egg-dumping" in the older literature) in waterfowl to be non-adaptive, either because it reflects abnormal behaviour ("loss of maternal instinct") or because it is a side-effect of competition for suitable nest sites in hole-nesting waterfowl (Erskine 1990). Semel and Sherman (2001) resurrected this idea and proposed a similar mechanism to account for "apparent" CBP in Wood Duck *Aix sponsa*. They proposed that some nest sites are preferred, perhaps because of their quality or because young females return to their natal nest on breeding for the first time. Contests for these nests ensue with more than one female laying eggs in the nest, but ultimately only a single female incubates the clutch. The usurped females become *de facto* parasites. Parasitism was not the focus of their behaviour and arises only as an inadvertent consequence of laying eggs and failure to establish final ownership of the nest (*i.e.* accidental parasitism).

However, several recent lines of evidence argue against the accidental parasite hypothesis as an explanation for CBP in waterfowl, and in other birds as well. First, several researchers (Eadie 1989; Pöysä 2003b; Odell & Eadie 2010) observed frequent parasitic egg-laying in nests in which eggs were added experimentally to empty nests without a host female being present. Hence, parasitic laying in these instances cannot be explained as a result of the laying female being "ousted" from the nest by the host female who incubates the eggs, since there was no host with whom to compete. Second, Eadie (1989) conducted removal experiments with Barrow's Goldeneye *Bucephala islandica* and Common Goldeneye *B. clangula* and found that, when the host female was removed, putative parasites continued to lay eggs but did not incubate the eggs, despite the fact that there was no female to prevent them from doing so. Conversely, when the parasitic females were removed, the hosts continued to lay and ultimately incubate the clutch, demonstrating that the different response by parasites was not simply due to an effect of experimental disturbance. This suggests that parasites and hosts behave very differently right from the outset.

Finally, recent work by Åhlund (2005) has demonstrated striking differences in the behavioural tactics of parasitic and host Common Goldeneye females at the nest: hosts and parasites differed in the timing of egg-laying, deposition of down, covering eggs on departure, and time spent on the nest as the egg-laying sequence progressed. These observations suggest that CBP is a genuine reproductive tactic and not just a consequence of nest site competition (Åhlund 2005). Similarly, recent experimental studies have revealed sophisticated responses of parasitically laying Common Goldeneye females to variation in nest (egg) predation risk (Pöysä 2003a; Pöysä *et al*. 2010), while other studies have demonstrated clear fitness advantages

of CBP for parasitically laying Common Goldeneye females (Åhlund & Andersson 2001). The fact that CBP occurs in such a large number of waterfowl species, many of which do not nest in tree cavities and do not compete for specific nests sites, argues against the accidental parasite hypothesis as a general explanation of this behaviour. These observations, together with the discovery that brood parasites often make fine-tuned, adaptive egg-laying decisions in waterfowl and other species (Brown & Brown 1991; Lyon & Everding 1996; Pöysä 1999; Lyon & Eadie 2008 and below), confirm that CBP is generally an adaptive alternative reproductive strategy in both waterfowl and other birds.

Traditional hypotheses

Adaptive hypotheses about the CBP have traditionally been classified into four types (summarised from Lyon & Eadie 2008) as follows:

Best-of-a-bad-job (BOBJ). According to this hypothesis, females lay eggs parasitically when they are unable to breed otherwise (constraint), or when environmental conditions are unfavourable such that the prospects for successful reproduction by nesting are low (restraint). A variety of ecological and physiological factors have been proposed to influence a female's ability to nest on her own, including nest site or territory limitation, body condition, age and experience.

Nest loss. A variant of the BOBJ hypothesis focuses on nest loss as the causative factor. Females that lose their nest to predation during egg-laying or early incubation may be able to lay some additional eggs (or may have eggs already developing in the ovary) but are not able (or it is not worthwhile) to establish a new nest. This hypothesis could be classified as a form of constraint (BOBJ), but many researchers have discussed it as a separate mechanism (and so we list it here in that form for comparison).

"Professional" or life-long specialist parasites. Under this hypothesis, females never raise their own young and only lay in the nests of other females. It is argued that these females have higher lifetime fitness (when rare in the population), because they are emancipated from the costs of parental care and so are able to invest in additional production of eggs. Under a game theoretic version of this hypothesis, negative frequency-dependent selection works to stabilise the frequencies of nesting and parasite females in the population (a mixed evolutionarily stable strategy; ESS).

Fecundity enhancement. This hypothesis posits that nesting females also lay some additional eggs parasitically and, by doing so, are able to increase fitness beyond that possible through nesting alone, presumably by bypassing some of the constraints or costs of raising the additional eggs/young on their own.

We were able to locate 17 studies that have attempted to test at least some of these hypotheses for waterfowl (Table 1). Of the four traditional hypotheses, no support has been found for either the nest loss hypothesis (0 of 5 studies that examined this hypothesis) or the life-long "professional"

Table 1. Summary of empirical studies in which the applicability of traditional hypotheses of conspecific brood parasitism (CBP) have been assessed. Tests of a specific best-of-a-bad-job hypothesis are given in parentheses.

Species	Hypotheses				Source
	Best-of-a-bad-job	Nest loss	Life-long parasite	Fecundity enhancement	
Bar-headed Goose	Yes		No	No	Weigmann & Lamprecht 1991
Snow Goose	Yes	No			Lank et al. 1989
Barnacle Goose	Yes				Forslund & Larsson 1995
Barnacle Goose	Yes			No	Anderholm et al. 2009
Maned Duck	Yes				Briggs 1991
Canvasback	Yes				Sorenson 1993
Redhead	Yes		No	Yes	Sorenson 1991
Wood Duck	Yes	No	No		Semel & Sherman 2001
Common Eider	No				Robertson et al. 1992
Common Eider	Yes/No			No	Robertson 1998
Common Eider	No (nest site limitation)			No	Waldeck et al. 2004
Common Eider	No (nest site limitation)				Waldeck et al. 2011
Common and Barrow's Goldeneye	Yes (nest site limitation)	No	No	Yes	Eadie 1989, 1991
Common Goldeneye	No (nest site limitation)	No			Pöysä 1999
Common Goldeneye			No	Yes	Åhlund & Andersson 2001
Common Goldeneye	No (nest site limitation)				Åhlund 2005
Ruddy Duck	No	No	No	Yes	Reichart et al. 2010

parasite hypothesis (0 of 6 studies) although the later may be difficult to detect given that it would be beyond the scope of most studies to follow a "pure" parasite throughout her entire lifetime (requires detailed observational data, recaptures, genotyping of all eggs in a population, *etc*.). Nonetheless, in most cases where females have been followed through time, they have been observed to switch between nesting and parasitism (or to use both strategies in the same year – dual nesters) suggesting that pure parasites, if they occur, are rare (Eadie 1989; Sorenson 1991; Åhlund & Andersson 2001; Reichart *et al*. 2010). To date, the hypotheses that are best supported are versions of the BOBJ hypothesis (10 of 16 studies) and, to a lesser extent, the fecundity enhancement hypothesis (4 of 8 studies; Table 1). Thus, at least for most waterfowl, there is support for the idea that some females pursue CBP due to constraint or restraint, whereas other females appear to do so to enhance total reproductive output. Few of these studies were able to determine which females did what. Perhaps the most interesting are the results of Åhlund and Andersson (2001) who showed that parasitic Common Goldeneyes comprised both females that only laid parasitically in a given season (pure parasites) and others that laid parasitically and also had a nest of their own (dual nesters). The reproductive "payoffs" varied considerably – dual nesters produced 1.5 times more offspring than non-parasitic (nesting) females and 2 times that of pure parasites. By combining parasitism with normal nesting, some females were able to double their reproduction. Similar patterns occur in

Common and Barrow's Goldeneyes in British Columbia (Eadie 1989; Jaatinen *et al*. 2009, 2011). Clearly, more than one hypothesis can apply to the same population. How best to make sense of the range of outcomes summarised in Table 1 is considered below.

A revised framework for future research

Lyon and Eadie (2008) pointed out that the traditional set of hypotheses are potentially confounded at several levels, conflating what a female does (nest, parasitize, or both) with fitness benefits of doing so, with ecological factors influencing her decision (nest loss, nest limitation, host availability, *etc*.), and finally with the evolutionary dynamics that maintain some frequency of CBP in the population (frequency-dependent ESS). Lyon and Eadie (2008) proposed a revision to the traditional set of hypotheses and they based this revision partly on a conceptual framework derived from Sorenson's (1991) reproductive decision model. Under this model, the ability to lay some eggs parasitically allows females to fine-tune reproductive investment because without the possibility of CBP, females are faced with an all-or-none decision to nest or not to reproduce at all. Key to this framework is the fundamental difference between two contexts of brood parasitism – parasitism by non-nesting females and parasitism by nesting females. For non-nesting females, parasitism allows for an intermediate investment between no reproduction and nesting. Thus, females prevented from nesting can gain some fitness through

parasitism where otherwise none would be possible. Parasitism by nesting females, in contrast, allows females to increase their reproductive effort when conditions are very good without entailing a full second nest effort. Parasitic egg-laying allows these females to adjust reproductive effort upwards in smaller increments to match expected returns.

This conceptual framework is a useful advance in two ways. First, it unifies all four possible nesting options (not breeding, parasitize only, nest only, parasitize and nest) as part of a single continuum that varies from low-to-high reproductive investment, and low-to-high expected fitness benefits. This captures the variation found both within and among species of waterfowl (Table 1). Second, parasitism can be combined with nesting in various ways over a female's lifetime to provide a flexible life-history, whereby females are able to modify their reproductive investment and options to variable ecological and social conditions. This framework moves the field forward from considering a large number of single independent hypotheses for each type of parasitism that intermix ecological factors, proximal influences, fitness benefits and evolutionary dynamics (the traditional framework; Table 1) into a more general life-history context with hypotheses that focus on the specific life-history trajectories of females and the expected fitness returns from pursuing those alternatives.

With this new framework, Lyon and Eadie (2008) proposed a modified categorisation of hypotheses for CBP, focusing on the three key fitness components: (a) current fecundity, (b) offspring survival, and (c) adult survival (*i.e.* future fecundity). Of particular importance is the distinction between parasites with and without their own nests because these two contexts likely involve different constraints, and different hypotheses may apply. Accordingly, there are three questions that must be addressed to understand the benefit of CBP: (a) does the female have a nest or not, (b) what fitness components and life-history trade-offs play a role in leading to increased fitness benefits via parasitism, and (c) what ecological, social, or physiological factors influence these trade-offs? Table 2 summarises Lyon and Eadies' (2008) revised hypothesis framework. Data are not available to test these hypotheses (few studies have followed the life-histories of individual parasites) and so we cannot place current studies in this new context. However, this is a new, more integrated framework for future studies of CBP in waterfowl and other birds. Perhaps the biggest requirement to improve understanding of this intriguing reproductive system is to determine more clearly what females are doing, both within a breeding season (nest, parasitize, or both) and among breeding seasons. Once a female's nesting status is determined, the context and suite of relevant hypotheses can be analysed more carefully and thus thoroughly evaluated (Table 2). This opens a wide range of new and intriguing questions about information use by the females which pursue these alternative pathways, and it is perhaps here where some of our newest insights on CBP have emerged. The second half of this review focuses on these new developments.

Table 2. A framework of hypotheses on the adaptive benefits of conspecific brood parasitism, modified from Table 1 in Lyon & Eadie 2008. This framework emphasises the distinction between hypotheses that apply to females without nests (strategy a) *versus* parasitizing females that also nested (strategy b).

Strategy	Mechanism	Fitness component enhanced	Traditional hypotheses
(a) Non-nesting parasite	**Egg production** (bypass costs of nesting and allocate more effort into egg production)	Current fecundity	Not emphasised; could explain life-long parasites
	Nest/territory limitation (unable to obtain a nest site or territory)	Adult survival and/or current fecundity	BOBJ (constraint, salvage strategy, nest limitation)
	Energy/condition/ experience (females in poor condition, young)	Adult survival	BOBJ (restraint, salvage strategy, energy limitation)
	Quality of brood rearing (parasites lay in high quality nests; good hosts/ safe sites)	Offspring survival	Nest predation could apply
(b) Nesting parasite	**Nest loss** (loss during egg-laying)	Current fecundity	BOBJ (constraint, salvage strategy, nest loss)
	Clutch size/brood size constraints (high quality females in excellent condition increase egg production, bypass brood size constraints)	Current fecundity and/or offspring survival	Fecundity enhancement Side-payment Dual nesting
	Cost of reproduction (reduce cost of care in own nest/brood to enhance future reproduction)	Adult survival	Not emphasised

Cues used by parasitic breeders

There is a long history of discussion about the distinction between signals and cues (see Danchin *et al.* 2008; Wagner & Danchin 2010). Signals are traits that have been designed by selection to convey information, whereas cues incidentally contain information but were not selected for that purpose (Maynard Smith & Harper 2003; Danchin *et al.* 2008). Information about the attributes of potential hosts or their nests are most likely cues, and signals might be expected in species where kin selection plays a role in facilitating the occurrence of CBP. Studies of obligate brood parasites nicely illustrate the importance of information use to parasitic tactics. Reproductive fitness for obligate parasites depends entirely on the success of their parasitic eggs, so there is strong selection to employ tactics that enhance the survival of the eggs and young. For example, obligate parasites often need to find nests of the right host species and collect information that enables them to time their laying to match that of the host's breeding cycle (Davies 2000). Although total female fitness in species with conspecific parasitism does not depend nearly as heavily on gains from parasitic eggs as obligate parasites, fitness from parasitism can nonetheless be substantial (Åhlund & Andersson 2001). Thus, whenever parasitism is a well-developed component of reproduction, we expect that the use of cues to select hosts will be important as well. The question then is whether conspecific brood parasites show tactics similar to those of obligate brood parasites and, if so, what

types of information are used when making choices about parasitism.

Cues can reflect characteristics of the physical environment or the social environment. Types of information of particular interest in the context of CBP are "personal information" and "social information". The former is the information obtained by an individual's own interaction with the environment (*e.g.* its experience or history, such as the failure of a previous breeding attempt), whereas the latter refers to information obtained by observing other individuals (*e.g.* their location, phenotypic condition and reproductive performance). Danchin *et al.* (2008) term social information and non-private personal information (*i.e.* the information accessible to other individuals) as "public information". Social information may also be based on signals, *i.e.* traits that evolve and are involved in true communication between individuals (see Danchin *et al.* 2008). However, the role of signals in CBP has not been addressed (for interspecific brood parasitism, see Parejo & Avilés 2007).

How might conspecific brood parasites use information to modify parasitic egg-laying behaviour adaptively? Three issues must be considered: 1) how do researchers test for evidence of cue use; 2) what behaviours might enable potential parasites to acquire information; and 3) what specific cues might be used? The last question further entails a nested series of choices that parasites might make, each involving a distinct cue or set of cues, such as: (a) what general area to use (habitat cues), (b) which nests or females to parasitize, and (c) when

to parasitize a host nest. In addition to these choices, parasites need to decide how many eggs to lay in a given nest and, if parasites also have their own nest, how many eggs to allocate to nesting *versus* parasitism. Information gained by parasites could influence any of these decisions and so it is important to clarify which aspect is being addressed. This in turn requires that researchers are thoughtful about their methodology and careful in interpreting the patterns observed.

Methods used to detect cue use

Three methods can be used to elucidate the tactics and cues used by brood parasites. Simplest is a comparison showing that parasitized and non-parasitized nests differ with respect to some attribute likely to be important to the success of the parasite, such as the quality of the territory, nest or host. However, this method provides somewhat weak evidence for parasitic tactics because the patterns may reflect the outcome of host defenses and not parasitic tactics. It also can be possible to obtain false positive evidence for non-random patterns of parasitism. For example, spatiotemporal clustering in attributes of host nests can result in patterns when data are analysed for the entire population but not at spatial and temporal scales that are relevant to the choices that individual parasites face (*e.g.* Lyon 1993; McRae & Burke 1996). To assess parasitic tactics properly, it may be necessary to understand the spatial and temporal patterns of parasitism and then assess the choices parasites make with respect to the pool of hosts that are actually available given the spatial and temporal constraints

on parasitism (Brown & Brown 1991; Andersson & Åhlund 2000). Monte Carlo randomisations provide one powerful method for assessing patterns of brood parasitism in this context (Emlen & Wrege 1986; Lyon 1993). McRae and Burkes' (1996) study of Moorhens *Gallinula choropus* highlights the value of controlling for the spatial pool of available hosts. Host-parasite relatedness was higher than expected at the population level but was not different from random expectation given the pool of hosts actually available to brood parasites. Controlling for the pool of potential hosts revealed that parasites were not specifically targeting relatives (McRae & Burke 1996). However, neither population comparisons nor contrasts that control for spatiotemporal patterns of potential hosts provide definitive evidence for which cues parasites actually use to select nests. The problem is that factors that correlate with parasitism may not be the actual cues that parasites use when choosing nests to parasitize. Only experiments manipulating putative cues provide fully convincing evidence for cue use. These experiments are rarely done, but they have been conducted in a few waterfowl species (see below).

How do females obtain information?

Studies addressing behavioural aspects of nest site selection in Barrow's Goldeneye and Common Goldeneye have revealed that females gather information by prospecting for potential nest sites prior to the next breeding season (Eadie & Gauthier 1985; Zicus & Hennes 1989; Pöysä *et al.* 1999). Pöysä (2006) found for the latter species that this behaviour is associated with CBP: nest

sites that were visited more frequently by prospecting females in year t had a higher probability of being parasitized in year $t + 1$, suggesting that parasites gather information through nest-site prospecting to target parasitic laying in particular nests.

Prospecting activity peaks after most nests have hatched (and ducklings have left nests), matching the time when cues of a successful nest (eggshell membranes and fragments; Fig. 2) are highly visible (J. Eadie, unpubl. data; H. Pöysä, unpubl. data). It is not

A. Wood Duck

(a) Not used (shavings, undisturbed)
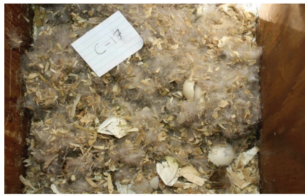
(b) Abandoned or laying (no down)

(c) Active incubation (down, eggs covered)

(d) Active incubation/laying (female, eggs, down)

(e) Successful hatch (shell membranes, egg caps)

(f) Failed/depredated (rotten, broken eggs, shells)

B. Common Goldeneye

(a) Successful hatch (7 ducklings hatched and left the nest)

(b) Successful hatch (9 ducklings hatched of 11 eggs and left the nest)

Figure 2. Examples of cues available in (A) Wood Duck nests and (B) Common Goldeneye nests after nesting. **A:** Wood Duck nests showing various stages of nesting, from not used (a) through to failed (f). **B:** Common Goldeneye nests showing two different examples of successful nests.

known if prospecting behaviour is associated with CBP in the Barrow's Goldeneye but, interestingly, prospecting activity seems to be higher at nest sites that had been parasitized earlier in the season (see Fig. 2 in Eadie & Gauthier 1985).

Prospecting behaviour is not restricted to hole-nesting species. Schamel (1977) mentions that preferred nest-sites are visited (prospected) regularly by non-breeding females throughout the summer (*i.e.* after hatching) in the ground-nesting Common Eider *Somateria mollissima*, another duck in which CBP is common (*e.g.* Robertson 1998; Waldeck *et al.* 2008). Fast *et al.* (2010) showed experimentally that nest-site materials left from the previous year influence the use of nest bowls by Common Eider females: nest bowls containing down were occupied earlier than control nest bowls with no down. As discussed by the authors, one explanation could be that nest down may indicate previous nest success and nest-site safety to females prospecting for nests. It would be interesting to study whether these aspects, *i.e.* prospecting behaviour and cues indicating previous nest success, are associated with the occurrence of CBP in the species.

Cues used by parasites to locate nests

Cues used by parasitically laying females to find and select suitable host nests have been studied extensively in the context of interspecific (obligate) avian brood parasitism. The main hypotheses can be classified as those dealing with nest placement (*e.g.* nest exposure, characteristics of the surrounding habitat) and those dealing with host behaviour (*e.g.*

conspicuous host behaviour, host activity; see Patten *et al.* 2011). While characteristics associated with nest placement in waterfowl may not be as diverse as they are in passerines, the most important group of host species for interspecific brood parasites, some general patterns emerge. First, CBP in waterfowl is more frequent in cavity-nesting species than in species that nest in emergent vegetation or upland (Rohwer & Freeman 1989; Sayler 1992; Eadie *et al.* 1998), implying that the ease in locating nest sites could play a role in CBP. Support for this idea also comes from cavity-nesting Wood Ducks where highly visible nest boxes are more frequently parasitized than less visible nest boxes (Semel *et al.* 1988; Roy Nielsen *et al.* 2006a; but see Jansen & Bollinger 1998 for a less clear effect). On the other hand, nest box visibility does not seem to affect the frequency of parasitism in another cavity-nesting duck, the Barrow's Goldeneye (Eadie *et al.* 1998). Similarly, Åhlund (2005, p. 434) mentions that parasitism rate does not differ between nests near the shore and nests further inland in the Common Goldeneye population he studied; visibility presumably differed considerably between the nest site types. In line with this, an experiment addressing nest site selection in Common Goldeneye revealed that females (potential parasites) prospect shore and forest boxes equally, irrespective of differences in the visibility of the nest boxes (Pöysä *et al.* 1999), suggesting that females are very capable at finding nest sites. Hence, while highly visible nest sites may be easier to locate, there must be other cues parasites use to locate and select nests.

Early observations suggested that parasitic females use the activity of other females (potential hosts) to locate nests. For example Weller (1959) describes several cases in which Redhead *Aythya americana* females apparently observed the nest-building and egg-laying activities of other females, leading the author to suggest that parasitic females used this behaviour to find nests. Similarly, several authors have suggested that Wood Duck females have a "decoying effect" on one another, leading often to heavily parasitized nests (Heusmann *et al.* 1980; Semel & Sherman 1986; see also Roy Nielsen *et al.* 2006a). Inspired by these observations Wilson (1993) carried out an experiment using Wood Duck decoys and found evidence for the hypothesis that parasitic Wood Duck females use the presence of conspecifics as a cue in the selection of nests. On the other hand, decoy nests with experimental eggs but no host were parasitized at the same rate as real nests that did have a host in Common Goldeneyes (Pöysä 2003b), Barrow's Goldeneyes (Eadie 1989) and Wood Ducks (Odell & Eadie 2010), suggesting that the presence of a conspecific host is not a necessary cue for parasites.

Cues used by parasites to select a nest

Location of potential nests for egg laying is the first step in the process of nest selection of parasites. However, not all of the located nests will eventually be parasitized (H. Pöysä, unpubl. data) suggesting that parasites actively select among potential nest sites. It is not always easy to make a clear distinction between these two steps in the process of nest selection, and the design of some studies does not allow a clear separation (see text on methodology above). In this section we consider only those studies that deal with the final step of the process, *i.e.* actual selection of nests by parasites, and review a variety of cues that have been identified.

Nest site quality or state

Empirical studies have explored several possible cues parasites may use to select a nest (Table 3). Several studies have addressed nest site characteristics while characteristics of the host female have received less attention. We are aware of only one study for waterfowl, on nest-box-breeding Common Goldeneye, in which both nest and host traits were considered, and nest site characteristics turned out to be more important than those of the host female (Paasivaara *et al.* 2010). Parasitism in relation to nest site quality has been well-studied in a non-waterfowl species, the Cliff Swallow *Hirundo pyrrhonota* (Brown & Brown 1991). Parasitic Cliff Swallows show remarkable sophistication in their ability to target host nests that are more likely to be successful than average, in part due to lower infestation by blood sucking nest parasites. Nest age was also identified as one cue used by parasitic females (Brown & Brown 1991): nest age may be a reliable indicator of the safety of a particular nest site.

Nest success and nest site safety, traits that do not necessarily mean the same thing, have been found to be associated with the occurrence of CBP in some waterfowl species but not in others (Table 3). For example, in the Common Goldeneye parasitism in a given year occurred more

frequently in nest sites that were not depredated (at least one duckling hatched and left the nest) during the previous nesting attempt than in nest sites that were either depredated or control nest sites (Pöysä 1999). A later study revealed a mechanism by which parasitically laying females identify safe nest sites, *i.e.* by nest site prospecting during the previous year (Pöysä 2006). Remnants of successful hatching of a clutch (see Fig. 2) thus seem to be important cues by which parasitic Common Goldeneye females select target nests. A critical prerequisite in this hypothesis is that nest success is predictable between successive breeding seasons, as found for Common Goldeneyes in which nest depredation is the main determinant of variation in breeding success (Pöysä 2006). Predictability of nest success, coupled with the ability of parasites to assess it and lay accordingly, make parasitic laying an advantageous evolutionary strategy (Pöysä & Pesonen 2007).

Roy *et al.* (2009) tested the nest success hypothesis for Wood Ducks and found, contrary to the prediction, that previously unsuccessful nest sites were more likely to be parasitized in the following year. These authors also found that previous success did not consistently predict future success. An important difference between this study and Pöysä's studies is that in the Wood Duck the main cause of failing was nest desertion, probably caused by a high rate of parasitic laying (Roy *et al.* 2009). If females are simply evaluating cues related to nest predation (*e.g.* broken eggs) a nest with a large number of deserted eggs may still indicate a safe nest with respect to predation risk, and be targeted by parasites. This would present an interesting situation of conflicting cues (predation risk or nest abandonment) and females might be predisposed to one source of information (a sensory trap). Alternatively, this pattern might result if parasitic egg-laying in deserted nests was more frequent because of a lack of host defence (*i.e.* at tended nests, hosts may prevent access whereas this would not be the case at untended nests). This highlights the difficulty of inferring cue use from patterns of nest use and only experimental studies are likely to tease these apart. At any rate, patterns of parasitic egg-laying in Wood Duck females did not correspond to patterns of nest success. The authors suggested that high nest density may have confounded the quality of information and caused parasites to make poor decisions (see Roy *et al.* 2009).

The nest success hypothesis also has been tested for Common Eider, and results suggest that parasitic females did not use nest-site safety as a cue for egg laying (Lusignan *et al.* 2010; Table 3). Specifically, Lusignan *et al.* (2010) found that nests in dense woody vegetation had the highest probability of survival but the lowest frequency of CBP. On the other hand, nests in highly visible artificial wooden nest shelters had the highest rate of parasitism and ranked second in terms of nest survival. This finding suggests that nest visibility had a greater effect on parasitism rate than nest site safety (see Lusignan *et al.* 2010).

Another way that parasitically laying Common Eider females could use cues to choose high quality nests was suggested by Ruxton (1999). He was inspired by the

Table 3. Empirical studies that have tested for evidence of the use of cues in the selection of nests by parasitically laying females. Type of cue and study (observational or experimental) are given, together with main findings. Interpretation of results and further comments according to original articles.

Species	Type of cue	Type of study	Support for cue use	Main finding and comments	Source
Common Goldeneye	Nest predation risk	Experimental	Yes	Parasitism more frequent in previously non-depredated nests	Pöysä 1999
Common Goldeneye	Nest predation risk	Experimental (simulation before egg laying)	No	Parasites did not respond to simulated depredation when laying in nests of which they did not have previous experience of success	Pöysä 2003a
Common Goldeneye	Nest predation risk	Experimental	Yes	Parasitism more frequent on lakes with low nest depredation risk	Pöysä 2003a
Common Goldeneye	Nest predation risk	Experimental (simulation during egg laying)	Yes/No	Parasites that experienced simulated partial clutch depredation stopped egg laying in the nest, whereas parasites that had not experienced it laid in the nest later in the season	Pöysä *et al.* 2010
Common Goldeneye	Nest success	Observational	Yes	Parasitism more frequent in previously successful nests	Pöysä 2006
Wood Duck	Nest success	Observational	Yes/No	Parasitism more frequent in previously unsuccessful nests	Roy *et al.* 2009
Common Eider	Nest-site safety/visibility	Observational	No	Nests with highest probability of survival had lowest frequency of parasitism (nest-site visibility more influential)	Lusignan *et al.* 2010

Table 3 (*continued*).

Species	Type of cue	Type of study	Support for cue use	Main finding and comments	Source
Common Goldeneye	Nest site traits	Observational (number of nesting attempts, occupation rate)	Yes	Probability of parasitism increased with the number of previous nesting attempts and occupation rate	Paasivaara *et al.* 2010
Common and Barrow's Goldeneye	Host presence	Experimental	No	Dummy nests that did not have a host were used and parasitized	Eadie 1989
Common Goldeneye	Host presence	Experimental	No	Dummy nests that did not have a host were equally parasitised as real nests with a host	Pöysä 2003b
Common Goldeneye	Host traits	Observational (nesting experience, condition)	Yes/No	Probability of parasitism increased with host nesting experience (and less clearly with host body condition) but, in general, host traits less important than nest site traits	Paasivaara *et al.* 2010
Wood Duck	Clutch size	Experimental	Yes	Parasitism more frequent in simulated nests with smaller clutch size (hatch success probably higher in smaller clutches)	Odell & Eadie 2010
Black Brant	Egg size	Observational	Yes	Parasitic eggs differed less in size from eggs in their host's nests than did random eggs placed in random nests	Lemons & Sedinger 2011
Common Eider	Host trait	Observational (condition)	No	Parasitized females were of same body mass as non-parasitized females	Waldeck *et al.* 2011

observation that predation rates were lower for parasitized Common Eider nests in one population (Robertson 1998). This finding, coupled with observations that nest depredation rates were correlated with female attentiveness (Swennen *et al.* 1993), led Ruxton (1999) to suggest that parasitically laying females could use variation in the female attentiveness at the nest during the egg-laying period as a cue of nest depredation risk and select target nests accordingly. The hypothesis predicts that there should be a positive relationship between an individual female's attentiveness at the nest during early egg-laying and her risk of parasitism (Ruxton 1999). To our knowledge this prediction has not been tested. It is important to note that nest attentiveness could also indicate female quality, making it difficult to distinguish between female quality and nest site quality because of the correlation between these two variables. Thus although it may be possible to correlate apparent cues (*e.g.* pattern of female nest attentiveness) with parasitic behaviour, we need to be careful to consider the underlying information that these patterns might represent (*i.e.* female quality). The "cues" that we measure may not necessarily be the cues that parasites perceive or respond to.

There are only a few studies in which cues affecting nest site selection and the laying decisions of parasites have been addressed experimentally (Table 3). In addition to Pöysä (1999, see above), two experimental studies have addressed the role of nest depredation risk and actual (partial) nest depredation in affecting the laying decision of parasites in the Common Goldeneye

(Pöysä 2003a; Pöysä *et al.* 2010). Those experiments revealed that parasitically laying females respond to varying degrees of nest depredation risk (*i.e.* they prefer laying in simulated nests that are in safe environments) but their response to simulated nest depredation varied depending on whether females experienced simulated partial clutch depredation (Table 3). These experimental findings suggest, first, that nest depredation and nest depredation risk are important cues, and second, that both personal information and social information are used in the selection of target nests by parasitically laying Common Goldeneye females. Other experimental studies have found that host presence was not an important cue in nest selection by parasitically laying Common Goldeneye (Pöysä 2003b) and Barrow's Goldeneye females (Eadie 1989).

Parasitic Wood Duck females appear to respond to variation in the number of eggs in a nest (Odell & Eadie 2010). In this study a choice of nests containing clutches of 5, 10, 15 or 20 experimental eggs was offered to Wood Duck females, and the number of eggs laid in the simulated nests declined in direct relation to the number of experimental eggs in the nest. This finding is of particular interest because it suggests the possibility that parasitically laying females are able to assess the number of eggs in a nest, a cue associated with important fitness consequences because large clutches often have low hatching success (Roy Nielsen *et al.* 2006b; Odell & Eadie 2010). Lemons and Sedinger (2011) report a remarkable pattern for the Black Brant *Branta bernicla nigricans* in which parasitic eggs match the size of host

eggs, suggesting that parasitically laying females recognise host egg size and lay accordingly, probably to improve hatching success. How they might do so is completely unknown.

Territory or host quality

The importance of host female quality (*i.e.* body condition) has been addressed in Common Goldeneyes and Common Eiders, and appeared not to be an important cue for parasitically laying females (Paasivaara *et al.* 2010; Waldeck *et al.* 2011). It should be noted that nesting schedule, a feature that also may reflect host female quality, has been found to be associated with the occurrence of CBP in many waterfowl species (*i.e.* clutches laid early in the season are more frequently parasitized than late clutches: Dow & Fredga 1984; Sorenson 1991; Robertson *et al.* 1992); however, other factors were not controlled in these studies (see Paasivaara *et al.* 2010). Older females often nest earlier and if CBP occurs more frequently early in the season, then a pattern would emerge of older (and perhaps more experienced or higher quality) females being parasitized disproportionately. The causative arrow could however be in the opposite direction: parasites might target older experienced females and, if older females nest earlier, then CBP would be more frequent in early nests. This would require careful experiments or statistical controls to decouple this pattern. Monte Carlo randomisation analyses could be used to determine if parasites selected non-randomly from among the host nests available, as noted above. Very few such tests have been conducted for waterfowl and

this remains an interesting and important direction for future work.

Timing of host laying cycle

Synchronising the timing of egg-laying with the host's laying cycle is thought to be important for interspecific brood parasites (Davies 2000) and for conspecific brood parasites as well. A role for host cues that reveal the timing of their cycle (but which have yet to be confirmed) has been found to be important in the few studies of non-waterfowl species that have examined these patterns while also taking random expectations into account (Emlen & Wrege 1986; Lyon & Everding 1996). Brown and Brown (1988) found that parasitic Cliff Swallows, which parasitize hosts by transferring eggs physically in their beaks, were remarkably good at synchronising timing with the host's laying and incubation period.

Matching the timing of egg-laying to a host's own clutch is particularly important in precocial birds such as waterfowl because the young hatch synchronously and leave the nest simultaneously within 24–48 h after hatching. Mismatched timing of egg-laying by the parasite can result in eggs failing to hatch, or young hatching after the host female has already left with her brood (see Bellrose & Holm 1994; review in Sayler 1992). Nonetheless, parasitic eggs are laid after the onset of incubation in several species (Jones & Leopold 1967; Clawson *et al.* 1979; Heusmann *et al.* 1980; Eriksson & Andersson 1982; Eadie 1989; Bellrose & Holm 1994; Šťovíček *et al.* 2013; review in Sayler 1992). Sayler (1992) describes a case of interspecific brood parasitism in which a parasitic Redhead female laid in a

Canvasback *Aythya valisineria* nest while it contained hatched ducklings. In contrast, Wood Ducks in some populations laid up to 80% of parasitic eggs prior to host incubation (Clawson *et al.* 1979).

Matching the timing of egg-laying with hosts has been documented in several non-waterfowl species, but more research would be useful to explore the cues and mechanisms used by parasites to fine-tune the timing of parasitic egg-laying and to understand better the constraints of doing so. To add further complexity, exciting new work by Hepp and colleagues has shown that even slight differences in incubation temperature can have significant impacts on the post-natal development and survival of young (Hepp *et al.* 1990, 2006; Kennamer *et al.* 1990; DuRant *et al.* 2010, 2011, 2012a,b). Thus, timing of egg-laying and incubation efficiency could have a large impact on parasite (and host) fitness. Odell (2008) found that eggs of parasitic Wood Ducks in California had higher levels of androgens than host eggs and this might accelerate the development of parasitic eggs laid at the end of the host laying period or after the initiation of incubation. Typically, host females spend large portions of the day on the nest during incubation, and yet parasitic females do not appear to use host presence as a cue to avoid these nests. Possibly, parasites cannot detect accurately the stage of incubation and simply the presence of another female or evidence of an active nest provides a sufficient incentive to induce egg-laying. Alternatively, cases of mismatched timing of laying with respect to the host's laying cycle might be influenced by host availability, for instance some females may have no potential hosts in the laying stage to parasitize when they have a parasitic egg ready for laying. A similar explanation may account for the fact that parasitic females will often lay eggs in deserted nests, occasionally leading to large accumulations of abandoned eggs (termed "dump nests" in the older literature). Sayler (1992) noted that parasitic Redhead females will often follow each other to nests and lay a series of eggs in those nests over several days. Similar behaviour has been observed in Wood Ducks (Semel & Sherman 2001) and Common Goldeneyes (Eadie 1989; Åhlund 2005). Sayler (1992) suggested that these nests appear active to parasitic females given the presence of other females and eggs being laid in the nest, even though the host has already abandoned the nest.

A curious (and opposite) pattern has been documented in Common Eiders. In several populations, researchers have found that parasitic eggs are often laid in nests *before* the host female begins to lay her own eggs. The host female thus lays her eggs in a nest in which another egg is already present, and then subsequently completes her clutch and incubates the nest. Common Eiders often reuse nest bowls in successive years and this pattern could be explained if females are simply competing for certain nest sites, with the first female being ousted (the accidental parasite). However, Robertson (1998) suggested that this phenomenon was due to nest takeover and adoption, possibly in response to nest predation risk. He reported that in nests where females took over nests, predation on the first eggs was lower than in comparable nests with only a single female (*i.e.* no takeover). Robertson (1998) argued

that the presence of an egg in a nest would indicate that the site was a safe nest location (since the egg had not been depredated), and therefore the nest may be attractive to another female. The benefit of obtaining a safe nest site could outweigh the potential cost of caring for the additional eggs. Ruxton (1999) further suggested that females can detect variation in the predation risk associated with different nests, and use this information to target nests with low predation risk as sites for laying parasitically, a hypothesis similar to Pöysä's (1999, 2003a, 2006; Pöysä *et al*. 2010) hypothesis to explain CBP in Common Goldeneyes. Waldeck and Andersson (2006), using protein fingerprinting techniques, found that another female laid before the host started laying in 41% of mixed clutches. Similarly, Hario *et al*. (2012) found that 58% of parasitic eggs in a population in Finland were the first or second eggs laid. Waldeck and Andersson (2006) reported that nests that were taken over have higher early survival than other nests, consistent with the hypothesis that CBP in Common Eiders is driven by selection for safe nest sites. It is still unclear whether "nest takeover" is a form of CBP at all, although it is often presented in that context (see discussion in Roberston 1998). Clearly, much more work remains to better understand the cues that parasitic females use to fine-tune the timing of egg-laying.

What determines the patterns of parasitism?

We have, to this point, focused on the cues that parasites use. This is not intended to imply that cues that hosts might use, and the role of hosts in determining the patterns or outcomes of parasitic interactions, are not important. Indeed, there are a number of decisions hosts might make to influence the occurrence of parasitism, each involving different cues. An analysis of host decisions is beyond the scope of our paper, and limited information is available. However, it will be important in future studies to integrate cue use and decision-making by hosts for several reasons: 1) it links cognition and decision-making to parasitism broadly; 2) decisions are linked in a game theoretic way that include both parasite and host responses (*e.g.* Andersson & Eriksson's 1982 clutch size model); and 3) for some decisions (*e.g.* who lays in a nest), it can be very difficult to determine whether the host or the parasite determines the outcome (and hence who is using what cues).

This last question is particularly germane in our efforts to understanding the relative roles that hosts and parasites play in determining the patterns of parasitism. While some authors emphasise the active role of hosts (*e.g.* Andersson & Åhlund 2000), others suggest that hosts do not play an important role (*e.g.* Pöysä 2004). Evidence that host-mediated facilitation does not play a central role in the laying decisions of parasites comes from experiments in which parasitic laying has been induced in simulated nests that do not have a host present (Pöysä 2003a,b; Odell & Eadie 2010; Pöysä *et al*. 2010). It is noteworthy that laying in simulated nests is frequent in Common Goldeneyes even when active real nests are available (H. Pöysä, unpubl. data), indicating that this behaviour is not simply due to a shortage

of host nests. Pöysä (2003b) specifically addressed the importance of host recognition by parasites in the selection of nests and found it not to be important. These experiments suggest that host females do not play an active role as facilitators of parasitism. However, the role of hosts in CBP remains uncertain. One issue that has recently been of growing interest, and is particularly relevant to the question of the role of hosts in facilitating CBP, is the potential influence of kinship amongst hosts and parasites.

A role for kinship?

The idea that hosts and parasites might be related, and hence that CBP is not a form of parasitism *per se*, but rather a cooperative behaviour facilitated by kin selection, was suggested over 30 years ago by Andersson (1984). In waterfowl, females are the philopatric sex so the premise of the kinship hypothesis is that females might return to their natal area and lay eggs in the nests of close kin. A central feature of the mechanism is that hosts are in the driver's seat. By allowing kin to lay eggs in the host nest, the host may be facilitating reproduction by a relative where otherwise none would have been possible, thereby increasing the hosts' own inclusive fitness. The idea was often cited but rarely tested until a number of new theoretical models revisited this idea (Zink 2000; Andersson 2001; Lopez-Sepulcre & Kokko 2002; Jaatinen *et al.* 2011a). The current consensus of these models is that kinship can facilitate CBP, provided that costs to the host are low and some degree of kin recognition exists (Lyon & Eadie 2000; Eadie & Lyon 2011). If

costs to hosts are high, then parasites should avoid laying eggs in a relative's nest so as not to reduce the host's fitness, and thereby lower the parasite's inclusive fitness. Testing the kin selection hypothesis requires detailed information not only on host-parasite relatedness, but also on the costs to the hosts, the degree (or existence) of kin recognition and the extent to which parasites *versus* hosts control or facilitate CBP.

A number of empirical studies using molecular genetic techniques (DNA microsatellites and isoelectric focusing of egg albumin proteins) have now documented high host-parasite relatedness in waterfowl, including the Wood Duck, Common Eider, Barrow's Goldeneye and Common Goldeneye (review in Eadie & Lyon 2011). However, the mechanisms leading to high host-parasite relatedness remain unknown, although kin recognition and discrimination against unrelated parasites by hosts have been suggested in the Common Goldeneye (Andersson & Åhlund 2000; but see Pöysä 2004). The finding that hosts and parasites are often related opens the possibility that parasites or hosts could recognise kin and that kinship could provide a cue in nest/host selection. Interestingly, Jaatinen *et al.* (2011b) found that the response of parasitic Barrow's Goldeneye females to relatedness depends on their nesting status: parasitic females that had a nest of their own ("nesting parasites") responded to relatedness by laying more eggs with increasing relatedness to the host, while non-nesting parasites did not respond to relatedness. The authors discuss several possible reasons why nesting and non-

nesting parasites differed in their response to relatedness but the mechanisms underlying this finding are currently unknown. Finally, Pöysä *et al.* (2014) provided experimental evidence that nest predation risk and interaction between related parasites are associated with kin-biased co-parasitism (related parasites non-randomly laying in the same nest) in the Common Goldeneye. In reviewing the evidence to date, the initial results suggest that kinship could play a role as a cue at least for parasites that have a nest of their own, but it remains to be determined whether kinship is a central driver in the evolution of CBP, or instead just one of several factors that influence the frequency and occurrence of this intriguing behaviour (Eadie & Lyon 2011).

Conclusions and future issues

Our understanding of CBP has advanced considerably in the 35 years since Yom-Tov (1980) first brought it to our attention, and research on waterfowl (Anseriformes) has contributed disproportionately to this knowledge. We now have a much better understanding of the ecological and social conditions under which CBP occurs, and over two dozen studies of waterfowl have tested the existing set of hypotheses proposed to account for this behaviour. Collectively, these studies support the hypotheses that CBP allows some females to reproduce when they otherwise could not, while other females use parasitic egg-laying as a way to enhance total fecundity. A life-history approach offers a new framework by which to integrate all of these possibilities into a theory of flexible life-history, and the set of traditional hypotheses for CBP can be readily integrated into this new framework. We suggest that this new framework will provide a useful direction and impetus for the next generation of studies of CBP, fuelled by an increasing battery of molecular genetic techniques and a growing array of technological tools to track females and their reproductive trajectories throughout their lifespan.

We have also focused on an emerging, exciting area for future investigations of CBP – namely the use of cues and information by conspecific brood parasites as they seek suitable places to lay their parasitic eggs. Recent empirical studies of CBP in waterfowl have revealed remarkable cognitive abilities in parasitic females, although the actual mechanisms remain unknown in most cases. In particular, the use of public information by parasites in locating and selecting nests that have high prospects of success is a promising avenue worth exploring to gain insight into the evolution of nest/host selection and egg laying decisions of parasites. Interestingly, the importance of public information has also been stressed recently in the context of interspecific brood parasitism; Parejo and Avilés (2007) suggested that parasites might eavesdrop on the sexual signals of their hosts to find high quality foster parents for their own offspring. The role of parental quality as a cue in CBP has received little support in waterfowl but more research on this aspect is needed. The ability of parasites to evaluate the number of eggs in a nest and to modify their own laying behaviour accordingly, as demonstrated with Wood Ducks, is intriguing and worth further exploration in other species.

The role that kinship plays as a cue in the laying decisions of parasites (and hosts) remains a challenging task for future studies. High host-parasite relatedness has been reported for several species, but it is unclear whether direct assessment of relatedness is involved or if some unmeasured correlate leads related females to select the same nest site. For example, as suggested by Pöysä (2004), high natal and nest site philopatry and preference of both hosts and parasites to lay in safe nest sites will also generate high host-parasite relatedness. Experimental studies and examination of the cost of parasitism to hosts and the ability of females to recognise or interact differentially with kin are required to disentangle these effects.

Acknowledgements

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