University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Faculty Publications in the Biological Sciences

Papers in the Biological Sciences

2004

Mark–recapture and behavioral ecology: a case study of Cliff Swallows

C. R. Brown
University of Tulsa, charles-brown@utulsa.edu

Mary Bomberger Brown
University of Tulsa, mbrown9@unl.edu

Mark–recapture and behavioral ecology: a case study of Cliff Swallows

C. R. Brown & M. B. Brown

Abstract

Mark–recapture and behavioral ecology: a case study of Cliff Swallows.— Mark–recapture and the statistical analysis methods associated with it offer great potential for investigating fitness components associated with particular behavioral traits. However, few behavioral ecologists have used these techniques. We illustrate the insights that have come from a long–term mark–recapture study of social behavior in Cliff Swallows (*Petrochelidon pyrrhonota*). The number of transient swallows passing through a colony per hour increased with colony size and was responsible in part for increased rates of ectoparasite introduction from outside the group into the larger colonies. Annual survival probabilities of males engaging in extra–pair copulation attempts were lower than those of males not seen to commit extra–pair copulations, suggesting that males who engage in this behavior may be inferior individuals and that females do not benefit from copulating with them. Females engaging in intraspecific brood parasitism had higher annual survival probabilities than ones either parasitized by others or not known to be either hosts or parasites. This suggests that parasitic females are high–quality birds and that brood parasitism is an effective reproductive tactic for increasing their fitness. By estimating first–year survival of chicks, we found that a clutch size of 4 eggs is often the most productive, on average, as measured by recruitment of offspring as breeders, although birds laying the more uncommon clutch size of 5 fledge more young on average. This helps to explain the observed clutch–size distribution in which clutch size 4 is the most commonly produced.

Key words: Clutch size, Coloniality, Parasitism, Social behavior.

Resumen

Marcaje–recaptura y ecología del comportamiento: el ejemplo de las golondrinas de frente canela.—El método de marcaje–recaptura y los métodos de análisis estadísticos asociados al mismo brindan un enorme potencial para investigar componentes del estado de salud asociados a determinados rasgos de comportamiento. Sin embargo, son pocos los ecólogos del comportamiento que han empleado dichas técnicas. En este artículo se presentan los resultados de un estudio a largo plazo de las golondrinas de frente canela (*Petrochelidon pyrrhonota*), en el que se empleó la técnica de marcaje–recaptura para analizar su comportamiento social. Observamos que cuanto mayor era el tamaño de la colonia, más elevado era el número de golondrinas que pasaba por la misma cada hora, siendo esto parcialmente responsable, en las colonias de mayor tamaño, de un aumento en las tasas de introducción de ectoparásitos desde fuera del grupo. Las probabilidades de supervivencia anual de los machos que intentaron llevar a cabo cópulas fuera de la pareja fueron inferiores a las de los machos a los que no se les había visto copular con una hembra distinta a la de su pareja, lo que sugiere que los machos que adoptan este comportamiento pueden ser individuos inferiores, y que las hembras no se benefician de copular con ellos. Las probabilidades de supervivencia anual de las hembras que participaron en parasitismo de nidada intraespecífico fueron más elevadas que las de aquellas que habían sido parasitadas por otras, o que las de aquellas que no eran conocidas como huéspedes ni como parásitas. Ello sugiere que las hembras parásitas son aves de alta calidad y que utilizan el parasitismo de nidada como una táctica reproductora eficaz para aumentar su buen estado de salud. La estimación de supervivencia de los polluelos durante el primer año de vida nos permitió determinar que una puesta de cuatro huevos suele ser, por término medio, la más productiva, medido

según el reclutamiento de polluelos como aves reproductoras, aunque las aves que tienen una puesta poco usual de cinco huevos se desarrollan, por término medio, a una edad más temprana. Esto ayuda a explicar la distribución observada del tamaño de las puestas, siendo la de cuatro huevos la que se produce con mayor frecuencia.

Palabras clave: Tamaño de la puesta, Colonialidad, Parasitismo, Comportamiento social.

Charles R. Brown & Mary Bomberger Brown, Dept. of Biological Sciences, Univ. of Tulsa, Tulsa, Oklahoma 74104, U.S.A.

Corresponding to: C. R. Brown. E–mail: charles-brown@utulsa.edu

Introduction

That the behavior of animals is adapted to the environmental or social conditions under which those animals live is a central tenet of behavioral ecology. Studying that adaptation usually requires measuring the fitness associated with a particular behavioral trait under particular ecological conditions. Although fitness is one of the most fundamental concepts in evolutionary biology dating back, in behavioral ecology at least, to W. D. Hamilton's (1964) work on social insects, there is debate about the best way to measure it in natural populations (Grafen, 1988). Fitness is probably best defined as the intrinsic rate of natural increase of a phenotype within a population, with the three major components of fitness being age at maturity, survival, and fecundity (Roff, 2002). The latter two parameters tend to be ones commonly measured in ornithological field studies, especially fecundity as reflected in annual nesting success. Most of the information on survival probabilities in natural populations has come from applied work done with wildlife management or conservation objectives.

Surprisingly few studies in behavioral ecology have directly measured either survival or lifetime reproductive success (a parameter based on survival) in relation to a behavioral trait of interest. For example, of the 117 papers published in 2002 in the field's premier journal *Behavioral Ecology* (volume 13), only three (2.6%) incorporated mark–recapture into their study design, and only one of those used modern statistical methods to analyze the data. Although some of these papers were based on laboratory studies for which mark–recapture may not have been appropriate, in many cases the same questions could have been addressed in the field and the behavioral traits under study linked to fitness. For example, mark–recapture methods permit estimation of survival associated with different mating strategies or different levels of sexual ornamentation and thus the estimation of fitness components associated with these different behavior patterns and their evolution. Many behavioral studies have tended instead to relate the expression of a behavioral trait to indirect correlates of fitness such as energetic gain (e.g., from foraging) or observed mating success (e.g., in comparing extra–pair mating strategies). In part, this has been because many studies in behavioral ecology have been short–term or exclusively experimental in focus, and have not followed large numbers of marked animals over multiple–time periods in natural environments.

In this paper, we illustrate the insights made possible by a long–term mark–recapture study of colonially nesting Cliff Swallows (*Petrochelidon pyrrhonota*), and how this work has furthered our understanding of questions in behavioral ecology. Our work focuses broadly on the adaptive significance of coloniality and the consequences of living in groups (colonies) of different sizes. Specifically, here we address how estimating the number of transient birds has been used in an experimental

study of between–group parasite transmission, how annual survival probabilities have provided information on alternative reproductive tactics such as extra–pair copulation and intraspecific brood parasitism, and how annual survival probabilities have been used to investigate tradeoffs associated with different clutch sizes. This paper reviews previously published empirical work, and additional methodological details (as well as other data and analyses) can be found in the original studies (Brown & Brown, 1998, 1999, 2004). We conclude by urging more behavioral ecologists to take advantage of mark–recapture methods and the many statistical analysis tools now available, particularly for studies that require estimation of fitness in relation to behavior.

Background

Cliff Swallows are highly colonial passerines that breed throughout most of western North America (Brown & Brown, 1995). They build gourd–shaped mud nests and attach them to the vertical faces of cliff walls, rock outcrops, or artificial sites such as the eaves of buildings or bridges. Their nests tend to be stacked closely together, often sharing walls. Cliff Swallows are migratory, wintering in southern South America, and have a relatively short breeding season in North America. They begin to arrive at our study site in late April or early May and depart by late July. They generally raise only one brood. Cliff Swallows are associated with a variety of ectoparasites, endoparasites, and viruses throughout their range (Monath et al., 1980; Scott et al., 1984; Brown & Brown, 1995; Brown et al., 2001). The ectoparasites, in particular the hematophagous swallow bug (Hemiptera, Cimicidae: *Oeciacus vicarius*), are responsible for much of the nestling mortality and nest failures that occur in our study area (Brown & Brown, 1986, 1996). We have studied ectoparasitism in Cliff Swallows by removing swallow bugs from nests by spraying (fumigating) them with a dilute solution of an insecticide, Dibrom, that is highly effective in killing swallow bugs.

Our study site is centered at the Cedar Point Biological Station (41°13' N, 101°39' W) near Ogallala, in Keith County, along the North and South Platte Rivers, and also includes portions of Deuel, Garden, and Lincoln counties, southwestern Nebraska, USA. We have studied Cliff Swallows there since 1982. There are approximately 160 Cliff Swallow colony sites in our 150 x 50 km study area, with about a third of these not used in a given year. Colony size varies widely; in our study area, it ranges from 2 to 3700 nests, with some birds nesting solitarily. Over a 20–year period, mean (± SE) colony size (*n* = 1363) was 363 (± 16) nests. Each colony site tends to be separated from the next nearest by 1–10 km but in a few cases by ≥ 20 km. In our study area, the birds nest on both natural cliff faces and artificial structures such as bridges, buildings, and highway culverts. The study site is described in detail by Brown & Brown (1996).

Transient birds and parasite transmission

A number of field studies on various taxa have shown that parasitism by ectoparasites (or infection by microparasitic pathogens) increases as group size or density increases (e.g., Brown & Brown, 1986; Moore et al., 1988; Rubenstein & Hohmann, 1989; Hieber & Uetz, 1990; Davies et al., 1991; Côté & Poulin, 1995; Hoogland, 1995; Arneberg et al., 1998; Krasnov et al., 2002). Although this seems to be a common pattern, we know little about the factors that cause it. One possibility is that larger groups of hosts represent a larger "target area" for parasites seeking hosts, and consequently more parasites successfully immigrate into areas with large concentrations of hosts. Another possibility is that once introduced into a group, parasites or pathogens are more easily spread by the greater spatial proximity of hosts in large colonies. The relative importance of these mechanisms has not been empirically investigated in any species, although epidemiological theory has recognized that immigration of parasites between host groups can be critical for sustaining epidemics and preventing local extinction of parasite populations (Cliff et al., 1981; Loehle 1995; White et al., 1996; Swinton et al., 1998; Grenfell et al., 2001).

Cliff Swallows show the typical increase in levels of ectoparasitism with group size; infestations of swallow bugs per nest increased significantly over an observed range of 1–1,600 nests in colony sizes (Brown & Brown, 1986, 1996). In addition, an encephalitis–related alphavirus (Buggy Creek virus) associated with Cliff Swallows also increased with colony size, as measured by per–nest infection probabilities of swallow bugs that vector the virus (Brown et al., 2001). Larger Cliff Swallow colonies contain more bugs for several possible reasons that include greater introduction of bugs into a colony from the outside, greater transmission of bugs within a colony, and larger colonies being more likely to be re–occupied by birds each year, promoting bug survival (Brown & Brown, 1996). In order to understand some of the mechanisms responsible for increased parasitism in larger groups, in 1999–2002 we experimentally measured the transmission of swallow bugs between colony sites in Cliff Swallows (Brown & Brown, 2004). We quantified transmission by fumigating entire colonies and counting the number of parasites appearing in the weekly interval between fumigations. This experiment showed that the number of bugs introduced into a colony per nest per week increased significantly with colony size (Brown & Brown, 2004), suggesting that at least some of the increased parasitism in larger Cliff Swallow colonies can be attributed to a greater likelihood of bugs being brought into a colony from outside the group.

The increased immigration of swallow bugs into larger Cliff Swallow colonies could occur because (1) more transient birds visit large colonies and/or (2) the transient birds visiting large colonies are more likely to be infested with dispersing bugs than are those visiting small colonies. Being wingless, bugs disperse only by clinging to the feet and legs of swallows that move from one colony to another; dispersal seems most likely to occur when a nest or entire colony site is not occupied in a given season, yet transient birds briefly visit those sites while investigating old nests. There is a relatively large pool of non–breeding Cliff Swallows in our study area in any given year, and these birds circulate among different colony sites, apparently assessing them for future years (Brown et al., 2000). These individuals are transients at each site in that they tend to be caught once at a colony, then vanish from that site sometimes to be caught again elsewhere.

We used mark–recapture to estimate the number of transient birds visiting colonies of different sizes. By setting mist nets across the upwind end of culverts containing nests, we caught birds as they exited the colony site. Days on which birds were captured at the experimental colonies (usually 3–3.5 hours with a net open per day) ranged from 9 to 33 at a site per season and extended from the period of the birds' arrival until most had departed from the colonies for the year. Total bird captures at the experimental colonies, in order of ascending colony size, were 529, 264, 613, 680, 2478, 2858, 3825, 4180, 4520, 5710, 3477, and 4149. All birds were banded with U.S. Fish and Wildlife Service bands upon initial capture (further details in Brown & Brown, 2004).

Transients are defined as birds not resident at a colony that pass through the site on a temporary basis. Those individuals caught only once at a colony include the transient class, but they also may include some residents who just happened to never be caught again. To estimate the fraction of the one–time captures that consisted of transients, we estimated the daily proportion of transients among those birds captured during each netting session with the method of Pradel et al., (1997). By fitting an age–dependent model to the capture data, the "first–year" age class approximates the transients, who, by virtue of not reappearing at a site, have much lower apparent survival, ϕ, than the residents who tend to be caught multiple times. The estimate of "first–year" survival allows one to calculate τ_t, the proportion of transients in each time interval $(_t)$, as $1 - (\phi_{1t} / \phi_{2t})$, where ϕ_{1t} is apparent survival probability of the "first–year" age class and ϕ_{2t} is apparent survival probability of the "older" age class (Pradel et al., 1997). The proportion of transients, τ_t, was multiplied by the number of newly caught birds during each capture session and divided by the number of hours that the net was open that day to produce the number of transients per hour per day. The calculation of τ_t for each netting session (Pradel et al., 1997) specifically excludes the fraction of one–time captures attributed to residents who were never caught again. Survival models were fit, and parameter estimates produced, by the program MARK (White & Burnham, 1999). Each colony was analyzed separately, as the number of capture occasions, dates of sam-

pling, and intervals between the occasions were different for each site.

For each colony, the best–fitting model (used to estimate τ_t) was usually one with time–dependent survival probabilities for the "first–year" age class, time–constant survival for the "older" age class, and time–dependent recapture probability the same among both age classes. Any differences in recapture probabilities among the different colonies (these tended to vary each day because of differences in weather conditions, time nets were open, etc…) were accounted for in the estimates of ϕ (and thus τ_t) calculated by MARK. See Brown & Brown (2004) for more details.

More transient Cliff Swallows passed through the larger colonies (fig. 1). Averaged over all days throughout the season, the total number of transient birds per hour per day increased significantly with colony size (fig. 1). This indicates that the increased ectoparasitism in larger colonies is attributable, in part, to more transient birds passing through those colonies. In addition, the weekly change in the average number of transients at a site tended to match the weekly change in the number of bugs introduced, indicating that transient presence is a determinant of bug immigration rates (Brown & Brown, 2004). Although there are other factors that also contribute both to the higher rates of between–group transmission and the increased overall incidence of parasitism in larger Cliff Swallow colonies (Brown & Brown, 2004), this analysis reveals that transient visitation of colonies is not uniform. Often considered a nuisance effect when one is trying to estimate survival of residents, the presence of transients in this case is biologically interesting. Formal mark–recapture models (e.g., Pradel et al., 1997) allow one to estimate the number of transients in a way that accounts for the fraction of resident birds who also were caught only once at a site. Without this approach, it would be impossible to estimate the total number of transient birds based strictly on how many times an individual was caught.

Annual survival and alternative reproductive tactics

One of the most striking realizations in behavioral ecology over the last two decades is that most animal populations contain individuals that parasitize the parental care provided to offspring by conspecifics. Parasitic exploitation of others occurs through both extra–pair mating and (in egg–laying species) intraspecific brood parasitism. Many studies have examined these reproductive tactics in various taxa, especially birds (e.g., Gladstone, 1979; Yom–Tov, 1980; Andersson, 1984; Rohwer & Freeman, 1989; Westneat et al., 1990; Field, 1992; Birkhead & Møller, 1992; Lyon, 1993; Brown & Brown, 1996, 1998, 2001; McRae, 1998). Much of this work has focused on determining the frequency, timing, and behavioral dynamics of these tactics in different populations and the socio–ecological contexts in which they occur. There is little information, however, on the
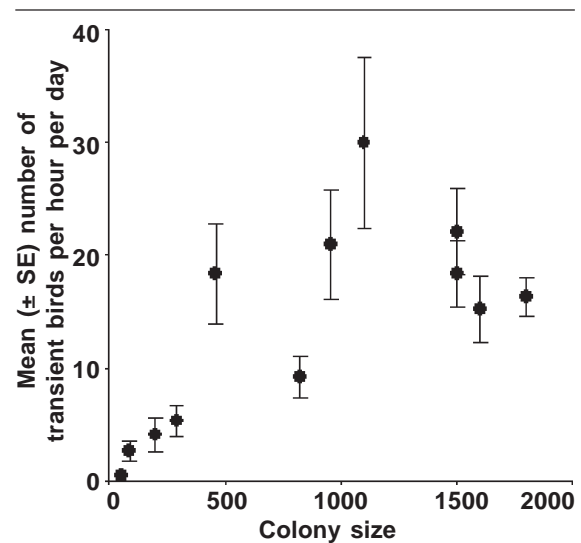

Fig. 1. Mean ($\pm$ SE) number of transient Cliff Swallows per hour per day over the entire nesting season in relation to Cliff Swallow colony size. The mean number of transient birds increased significantly with colony size ($r_s = 0.66$, $P = 0.02$, $n = 12$ colonies). Total sample sizes (number of birds caught) used to generate the estimates of the number of transients are given in the text (Brown & Brown, 2004).

Fig. 1. Promedio ($\pm$ EE) de golondrinas de frente canela transeuntes, por hora y día, a lo largo de toda la estación de nidificación según el tamaño de la colonia. El promedio de aves transeuntes aumentó significativamente con el tamaño de la colonia ($r_s = 0,66$, P = 0,02, n = 12 colonias). En el texto se detallan los tamaños de muestras totales (número de aves capturadas) empleados para generar las estimaciones del número de aves transeuntes (Brown & Brown, 2004).

long–term fitness consequences associated with extra–pair mating or brood parasitism. For example, is brood parasitism a last–ditch tactic used by inferior individuals who cannot establish their own nest or provide acceptable levels of parental care, or is it an effective supplemental reproductive strategy used by superior individuals to enhance their inclusive fitness? Are there tradeoffs between increasing short–term reproductive success and suffering long–term survival costs that result from, for example, an increased energetic expenditure, greater exposure to sexually transmitted diseases, or increased vulnerability to predation? Answering these questions requires estimating components of fitness associated with extra–pair mating and intraspecific brood parasitism, such as annual survival probability.

Extra–pair copulation

Extra–pair copulation in Cliff Swallows occurs in two contexts: among birds away from nest sites while they gather mud for nest construction and among neighboring birds while at nests (Brown & Brown, 1996, 1998). Neighbors engage in extra–pair copulations when a male trespasses into a nearby nest during the male owner's absence. Other males regularly patrol the mud–gathering sites and attempt extra–pair copulations with females who come there to collect nesting material. Most extra–pair copulation attempts seem to be initiated by males, and females may or may not resist. Extra–pair copulations are attempted both by males who are resident in a colony, maintaining a nest and mate of their own, and by nonresidents who circulate among colony sites (Brown & Brown, 1996). Because nonresidents are difficult to catch and color–mark, our data on survival came from resident males only. We made observations of extra–pair copulation attempts at two colonies where we could get close enough to the mud–gathering sites to identify color marks (paint stripes on the birds' white forehead patches) of resident males that perpetrated the copulation attempts. Other observations were made on color–marked males while watching birds at their nests in these same colonies. Any color–marked male seen to engage in at least one extra–pair copulation attempt was designated an EPC male, whereas color–marked males in the same colonies not seen to engage in any extra–pair copulation attempts were classified as non–EPC males. For analyses involving extra–pair copulations (and brood parasitism, below), we used cohorts initially marked from 1983–1987 with recaptures extending through 1995. Annual survival was modeled with EPC males ($n = 76$ birds) and non–EPC males ($n = 103$ birds) as separate groups versus as a combined group. Recapture probability in all models was time–dependent. The best–fitting model (AIC of 634.8 compared to next lowest of 642.8) was one with EPC and non–EPC males as separate groups, and from this model we estimated annual survival probability ($\pm$ SE) as 0.413 ($\pm$ 0.040) for EPC males and 0.614 ($\pm$ 0.055) for non–EPC males (Brown & Brown, 1998). Thus, annual survival of males engaging in extra–pair copulations was only about two–thirds that of males not seen to mate with extra–pair females. There appeared to be no other phenotypic differences (such as body mass) between the two classes of males that might have accounted for these results (Brown & Brown, 1998).

The lower annual survival probability for males that engaged in extra–pair copulations might mean that extra–pair mating is costly for males, perhaps through increased risk of sexually transmitted diseases (Sheldon, 1993; Lockhart et al., 1996). More likely, however, the difference in survival probability reflects inherent male quality (Brown & Brown, 1998). If so, females who mated with these males via extra–pair copulations did so with relatively inferior partners. This result is in contrast to both the widely held view that extra–pair copulations represent a way for females to achieve matings with males of high genetic quality (e.g., Westneat et al., 1990; Birkhead & Møller, 1992; Wagner, 1993; Jennions & Petrie, 2000) and field data on other species showing that longer–lived, more experienced, or "better" males are more likely to achieve extra–pair copulations (e.g., Kempenaers et al., 1992; Wagner et al., 1996; Weatherhead & Boag, 1995). In Cliff Swallows, extra–pair mating may be a "best–of–a–bad–job" strategy for inferior males, with deleterious consequences for females who participate either willingly or unwillingly (Brown & Brown 1998). This insight was made possible only by relating the behavior to annual survival probability using mark–recapture, and this study remains one of the few (if not only one) to measure long–term survival of males who do and do not exhibit this alternative reproductive tactic.

Intraspecific brood parasitism

Cliff Swallows commonly brood–parasitize nests with up to 20% or more in some colonies containing an egg laid by another female. All known cases of brood parasitism have been by females who were resident in the colony and maintained nests of their own, and parasitized nests are usually within a five–nest radius of the parasite's own nest (Brown & Brown, 1989, 1991). Cliff Swallows parasitize nests in two ways: by laying eggs in nests during the host's laying period and by physically moving eggs from the parasite's nest to a host's. Parasites time their laying or transfer of eggs to coincide with the host's own laying stage, such that parasitic eggs hatch synchronously with the host's. By observing color–marked birds at their nests and determining which individuals were consistently associated with a particular nest (thus owning it), we designated parasitic females as those seen laying or transferring eggs into a nest not their own. Host females were those in the same colonies whose nests were seen being parasitized by another bird or whose nests were found to be parasitized based on nest–check data. Daily or bi–daily checks of nest contents allowed us to infer instances of parasitic laying as cases where two or more eggs appeared per 24–hour period, and egg transfer as cases where an egg appeared in a nest during the host's incubation period but hatched synchronously with the host's eggs (Brown & Brown, 1998). Birds designated as neither hosts nor parasites were those color–marked individuals who were not observed to either parasitize others or be parasitized and whose nests showed no evidence of brood parasitism from nest checks. Additional details on how we designated the different classes of females are provided in Brown & Brown (1998).

Annual survival was modeled with four groups of females: those known to be parasites ($n = 17$), host females parasitized by laying ($n = 32$), host females parasitized by transfer ($n = 25$), and females not known to be parasites or hosts ($n = 65$). A model with both survival and recapture probability depend-

ent on female status was the best fit, with a lower AIC value (435.9) than a model with no effect of female status on survival (AIC = 438.1; Brown & Brown, 1998). From this, we estimated annual survival probability ($\pm$ SE) as 0.761 ($\pm$ 0.055) for parasitic females, 0.289 ($\pm$ 0.082) for host females parasitized by laying, 0.595 ($\pm$ 0.076) for host females parasitized by transfer, and 0.686 ($\pm$ 0.045) for females that were neither parasites nor hosts (Brown & Brown, 1998). Parasitic females thus had the highest annual survivorship and host females who had parasitic eggs laid in their nests the lowest.

These results suggest either that brood parasitism is a reproductive tactic used by high–quality females who are likely to live longer for that reason, or that parasitizing others reduces the cost of parental care to the extent that survival of the parasitic females is increased. The latter seems less likely because parasitic females maintain nests of their own and raise normal–sized clutches in their own nests (Brown & Brown, 1998). High–quality individuals will be those who have the necessary resources (time, energy) to parasitize their neighbors at little cost to themselves and at the same time have higher annual survivorship. Host individuals, on the other hand (especially those parasitized by laying), may be inferior individuals, and it is perhaps for this reason that they are parasitized. Parasitism only occurs when a nest is left unattended momentarily, and if host females are, for example, inherently inferior foragers, they may more often leave their nests unguarded because they take more time to find food.

In addition to higher personal survival of the parasitic females, we found that offspring from the parasites' own nests had higher first–year survival (as measured to their first breeding season) than birds raised in all other nests (Brown & Brown, 1998). With more of the young that they themselves rear surviving and with their own breeding lifespan being longer, the consequence is higher fitness for parasitic females. These females have an estimated lifetime reproductive success almost twice that of any other class of females (hosts, non–parasites, non–hosts; Brown & Brown 1998). Brood parasitism, at least as a supplemental reproductive strategy, would presumably spread in the Nebraska population if it wasn't regulated by extensive nest–guarding by most individuals. The cost of being parasitized and thus raising an unrelated chick seems to have selected for intense nest–guarding in Cliff Swallows. With such high levels of nest–guarding, potential parasites often simply do not have the opportunity to parasitize nests because relatively few are ever left unattended by an owner.

These results represent one of the few attempts to measure the long–term fitness consequences of intraspecific brood parasitism in any bird, and, as with those on extra–pair copulation in Cliff Swallows, they tend to go against conventional wisdom. Intraspecific brood parasitism is sometimes thought to represent a last–ditch strategy used by inferior females who were not successful in competing for nest sites or territories (e.g., Lyon, 1993; McRae, 1998; Sandell & Diemer, 1999). To the contrary, brood parasitism in Cliff Swallows is an effective tactic used by superior individuals to enhance their fitness. Using mark–recapture to estimate annual survival of different classes of individuals in Cliff Swallows has provided insights into the evolution of alternative reproductive tactics that would not have been possible from behavioral observations alone.

The evolution of clutch size

A major paradox in behavioral ecology is that in many species of birds, females typically lay fewer eggs and thus have fewer offspring than they can actually rear. Experiments have shown that the most productive clutch size, that is, the one yielding the most offspring surviving to fledge, is often not the most common (Klomp, 1970; Stearns, 1992; VanderWerf, 1992), and the most common clutch size is often smaller than the most productive. The most popular explanation for this paradox was that of Lack (1947, 1954), who argued that selection should favor birds that lay the most productive clutch size, and that the most common clutch size is in fact the most productive. This is because the larger clutches, while perhaps yielding more offspring to fledging, do not produce more eventual recruits into the breeding population because the chicks fledging from those large clutches may be in poorer shape and less likely to survive their first year. Furthermore, parents who lay and tend the larger clutches may themselves be less likely to survive to breed again, owing to the stress and additional work involved in raising a larger clutch. Thus, their fitness will be reduced, and there will be selection against laying the larger clutch sizes.

Lack's (1947, 1954) views on clutch–size evolution have been popular despite relatively little empirical support. In part, this has been because most studies, while often measuring fledging success associated with different clutch sizes and frequently in an experimental context, have not followed birds over multiple years to estimate either first–year recruitment or parental survival, and the few that have attempted this have not used modern mark–recapture statistical methods.

We studied clutch size in Cliff Swallows by doing daily or bi–daily nest checks at colonies throughout the study area, using a dental mirror and small flashlight inserted through each nest's mud neck. We defined clutch size as the maximum number of eggs ever recorded in a nest. Nests were monitored throughout incubation until hatching. Once hatching date was determined, we returned to the nest when the nestlings were 10 days old. At that time they were banded; their subsequent survival in later years was monitored through our long–term, extensive mist–netting at different colony sites in the study area. We recorded clutch–size data for 8,835 nests distributed among colonies of all sizes. Further details are provided in Brown & Brown (1999).

Cliff Swallows most often lay clutches of 4 eggs, but 3 eggs are also common (fig. 2). Five–egg clutches are uncommon (and those of 6 eggs so rare that they are not considered further). This overall clutch–size distribution (fig. 2), taken from all nests in our population during 10 years between 1982 and 1997, was similar to that for each year separately (Brown & Brown, 1999). Cliff Swallows exhibit the typical clutch–size paradox, with the average number of young surviving to fledge increasing steadily across the clutch size range of from 1 to 5 eggs in both fumigated nests (where ectoparasites had been removed) and nests exposed to natural levels of ectoparasites (Brown & Brown 1999; also see fig. 3). Thus, if more young are fledged on average from clutch size 5, why are clutches of 5 eggs so uncommon (fig. 2)?

One fitness component associated with clutch size is the number of offspring recruited as breeders in the year(s) following fledging. This can be determined by knowing how many chicks fledge from nests with a given brood size and estimating the average first–year survival probability associated with that brood size (Cliff Swallows breed as yearlings). Multiplying the number fledged by the probability of surviving the first–year gives an index of annual reproductive success (Brown & Brown, 1999).

For birds under natural conditions (exposed to ectoparasites), an age–stratified (age 1 vs all others), fully time–dependent model with three groups corresponding to brood sizes of 1–2, 3–4, and 5 best described first–year survival; this model had an AIC value of 5313.2, compared to an AIC value of 5322.4 for an otherwise equivalent model but without a brood–size effect (Brown & Brown, 1999). The time–dependence in first–year survival probabilities indicates yearly variation in the payoffs potentially associated with laying different numbers of eggs; we found that birds from brood sizes 1–2 had the highest first–year survival in three years, birds from brood sizes 3–4 had the highest first–year survival in four years, and birds from brood size 5 had the highest first–year survival in four years (Brown & Brown, 1999).

Annual reproductive success, as measured by the number of young surviving to the following season, varied with clutch size depending on each season's climatic conditions. In relatively cool seasons (as measured by daily high temperatures in June, the month of most brood–rearing in the study area), growth of ectoparasitic swallow bug populations in nests is slowed, as generation time is temperature–dependent. In such years, birds rearing broods of 5 had markedly higher annual reproductive success than those with smaller brood sizes (fig. 3A). However, in a more "average" year, climatologically, the advantage of a brood of 5 disappeared, with broods of 4 and 5 doing equally well (fig. 3B), and in a warm year, birds with broods of 5 did worse than those with either broods of 3 or 4 (fig. 3C). Interestingly, in all years, broods of 5 fledged the most offspring (fig. 3), contributing to the apparent clutch–size paradox had only fledging success been measured. Yet when
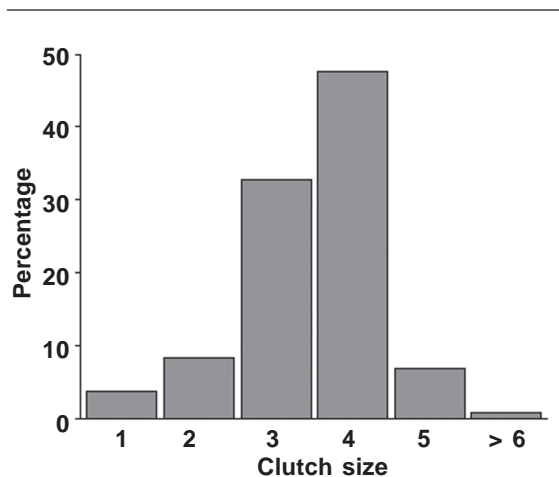

Fig. 2. Percentage distribution of Cliff Swallow clutch sizes, pooled across all years, *n* = 8,835 nests (Brown & Brown, 1999).

Fig. 2. Distribución porcentual de los tamaños de puesta de las golondrinas de frente canela, obtenidas en todos los años, n = *8.835 nidos (Brown & Brown, 1999).*

longer–term survival was measured through mark–recapture and related to climatic conditions, the perennial advantage of clutch size 5 disappeared.

The greater uncertainty associated with larger clutches is probably the key to explaining the observed clutch–size distribution in Cliff Swallows (fig. 2). Whenever birds cannot predict climatic conditions during brood–rearing at the time they lay eggs (which is likely the case with Cliff Swallows), the safest strategy is a risk–averse one of going with the clutch size that, on average, is likely to be best. Laying a clutch of 5 eggs potentially results in a relatively large payoff if the season turns out to be cooler than average, but if it is warmer than average, there is a serious fitness cost associated with that clutch size. In an average year, clutches of 4 do as well as those of 5, so it appears that the least risky strategy is to lay 4 eggs, the most common clutch size. A similar conclusion was reached by Boyce & Perrins (1987), who found that the reduced fitness for Great Tits (*Parus major*) rearing large clutches in the occasional bad years was enough to select for smaller average clutches than could be produced in good or average years. Others have also suggested that higher variance in fitness associated with larger clutches will result in selection for smaller clutches (Mountford, 1973; Yoshimura & Shields, 1992; DeWitt, 1997).

These analyses illustrate the utility of mark–recapture in studying the age–old clutch–size paradox. Experimental manipulations of clutch sizes provide evidence on the capability of parents to rear different numbers of chicks, but unless these offspring (and
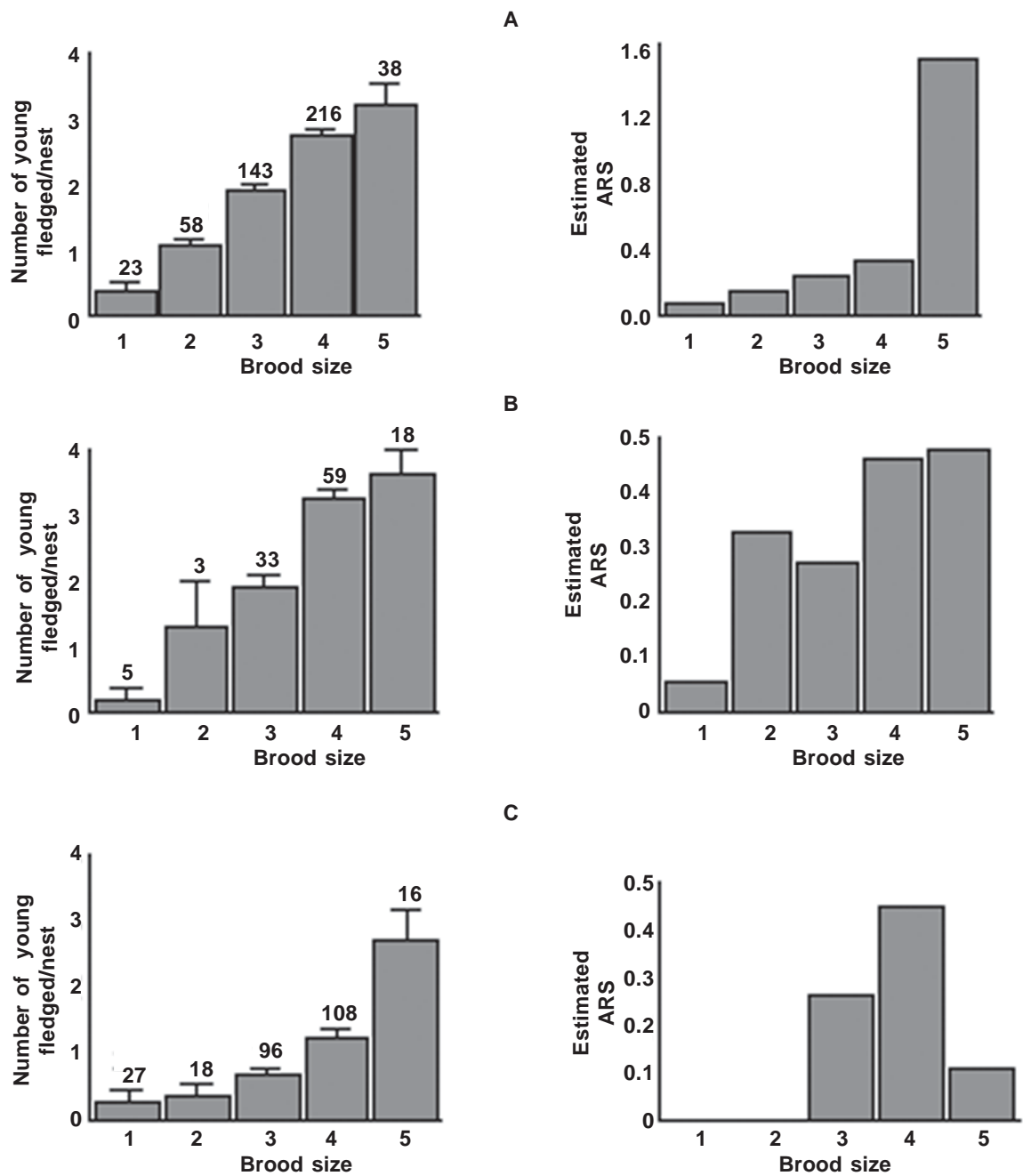
Fig. 3. Mean (± SE) number of nestling Cliff Swallows fledged and estimated annual reproductive success (ARS) in relation to brood size in: A. 1982, a cool season; B. 1990, an average season; C. 1988, a warm season, during June while broods were being reared. Annual reproductive success was estimated by multiplying the average number of chicks fledged by first–year survival probability for each brood size. Numbers above error bars indicate number of nests studied (Brown & Brown, 1999).

Fig. 3. Promedio (± EE) del número de pollos que salen del nido de golondrinas de frente canela y éxito reproductivo anual (ARS) estimado según el tamaño de la nidada en: A. 1982, una estación fresca; B. 1990, una estación media; C. 1988, una estación cálida, durante junio, mientras se criaba la nidada. El éxito reproductivo anual se estimó multiplicando el promedio del número de pollos que salen del nido por la probabilidad de supervivencia durante el primer año de vida para cada tamaño de nidada. Los números situados encima de las barras de error indican el número de nidos estudiados (Brown & Brown, 1999).

the parents) are followed over multiple seasons and their survival estimated, the long–term tradeoffs of clutch size cannot be known. The number of studies that have done this is still quite small.

Prospectus

As with all mark–recapture studies, there are challenges inherent in the application of mark–recapture methods to behavioral questions, and two stand out as particularly relevant to behavioral ecology. One is distinguishing mortality from dispersal. This is always a problem with open populations, because individuals permanently departing from a study area will be classified as dead. Various methods exist to estimate the fraction of individuals missed (Barrowclough, 1978; Payne, 1990; Marshall et al., 2004), and this is a particularly serious problem if the research objective is to determine absolute survival probabilities, perhaps for management or conservation purposes. In some cases, extent of dispersal might be related to the behavioral variable of interest; for example, individuals who do not attract mates might travel more widely than ones who are mated. However, if permanent emigration does not differ among the groups being compared, one can still achieve estimates of relative survival probabilities among groups of individuals that differ with respect to the behavioral covariate of interest. One way to determine whether emigration differs among groups is to examine the extent of movement of individuals with different behavioral traits within a study area of moderate size, as, for example, we did in a survival study of Cliff Swallows whose ectoparasites had and had not been removed the previous year (Brown et al., 1995). Since there was no evidence that the two groups differed in extent of dispersal, mark–recapture provided appropriate relative measures of survival that could be related to extent of ectoparasitism.

The other challenge for behavioral ecologists is coping with uncertainty in categorizing covariates associated with each individual. For example, we designated male Cliff Swallows as engaging in extra–pair copulations or not based on whether we saw them do it. Similarly, Cam et al. (2002) designated Black–legged Kittiwakes (*Rissa tridactyla*) as squatters or non–squatters based on whether individuals were seen squatting. In each case, however, since the animals could not be monitored continuously, some may have been misassigned as not having exhibited the behavior of interest when in fact they did show the behavior but it was undetected. Statistical methods exist for the modeling of unobservable and misclassified states (Kendall & Nichols, 2002; Kendall, 2004). Another solution is to consider the testing for differences among groups as conservative since it is "polluted" by misclassifications (Lank et al., 1990; Brown & Brown, 1998); if a difference is found, it is likely of sufficient strength to overcome the misclassifications.

Despite these potential challenges, mark–recapture studies and their associated statistical analyses have great potential applicability to behavioral ecology. Rigorous estimates of survival in natural populations enable us to specify the fitness consequences associated with a particular behavior in a direct and evolutionarily meaningful way that does not require (usually untested) assumptions about indirect correlates of fitness. This requires, of course, a long–term approach in which individuals are followed over multiple seasons and too often the surmounting of financial or other logistical obstacles to conducting long–term field studies (e.g., Tinkle, 1979; Nisbet, 1989; Malmer & Enckell, 1994). The insights that result, however, can often be worth the time and effort, as we have found for Cliff Swallows.

The use of multistate models (Nichols & Kendall, 1995; Lebreton & Pradel, 2002) to infer probabilities of movement also offers great potential for behavioral ecology. Estimating the likelihood of an animal moving from one site to another is essentially a measure of dispersal, and can reveal patterns of space use that are otherwise difficult to discern. We used multistate movement probabilities, for example, to study colony choice in Sociable Weavers (*Philetairus socius*), finding that individuals showed preferences to settle in colonies of size similar to that they had used previously (Brown et al., 2003). This enabled us to go beyond anecdotal observations on where certain banded individuals were found and allowed the testing of explicit hypotheses about the decision rules these birds use to choose colonies. We hope that these sorts of approaches will become more common in behavioral ecology.

References

Andersson, M., 1984. Brood parasitism within species. In: *Producers and scroungers: strategies of exploitation and parasitism*: 195–228 (C. J. Barnard, Ed.). Croom Helm, London.

Arneberg, P., Skorping, A., Grenfell, B. & Read, A. F., 1998. Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society of London* B, 265: 1283–1289.

Barrowclough, G. F., 1978. Sampling bias in dispersal studies based on finite area. *Bird–Banding*, 49: 333–341.

Birkhead, T. R. & Møller, A. P., 1992. *Sperm competition in birds*. Academic Press, London.

Boyce, M. S. & Perrins, C. M., 1987. Optimizing Great Tit clutch size in a fluctuating environment. *Ecology*, 68: 142–153.

Brown, C. R. & Brown, M. B., 1986. Ectoparasitism as a cost of coloniality in Cliff Swallows (*Hirundo pyrrhonota*). *Ecology*, 67: 1206–1218.

– 1989. Behavioural dynamics of intraspecific brood parasitism in colonial Cliff Swallows. *Animal Behaviour*, 37: 777–796.

– 1991. Selection of high–quality host nests by parasitic Cliff Swallows. *Animal Behaviour*, 41: 457–465.

– 1995. Cliff Swallow (*Hirundo pyrrhonota*). In: *Birds of North America*: no. 149 (A. Poole & F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

– 1996. *Coloniality in the Cliff Swallow: the effect of group size on social behavior*. Univ. of Chicago Press, Chicago.

– 1998. Fitness components associated with alternative reproductive tactics in Cliff Swallows. *Behavioral Ecology*, 9: 158–171.

– 1999. Fitness components associated with clutch size in Cliff Swallows. *Auk*, 116: 467–486.

– 2001. Avian coloniality: progress and problems. *Current Ornithology*, 16: 1–82.

– 2004. Empirical measurement of parasite transmission between groups in a colonial bird. *Ecology*, 85: 1619–1626.

Brown, C. R., Brown, M. B. & Danchin, E., 2000. Breeding habitat selection in Cliff Swallows: the effect of conspecific reproductive success on colony choice. *Journal of Animal Ecology*, 69: 133–142.

Brown, C. R., Brown, M. B. & Rannala, B., 1995. Ectoparasites reduce long–term survival of their avian host. *Proceedings of the Royal Society of London* B, 262: 313–319.

Brown, C. R., Covas, R., Anderson, M. D. & Brown, M. B., 2003. Multistate estimates of survival and movement in relation to colony size in the Sociable Weaver. *Behavioral Ecology*, 14: 463–471.

Brown, C. R., Komar, N., Quick, S. B., Sethi, R. A., Panella, N. A., Brown, M. B. & Pfeffer, M., 2001. Arbovirus infection increases with group size. *Proceedings of the Royal Society of London* B, 268: 1833–1840.

Cam, E., Cadiou, B., Hines, J. E. & Monnat, J. Y., 2002. Influence of behavioural tactics on recruitment and reproductive trajectory in the Kittiwake. *Journal of Applied Statistics*, 29: 163–185.

Cliff, A. D., Hagget, P., Ord, J. K. & Versey, G. R., 1981. *Spatial diffusion: an historical geography of epidemics in an island community*. Cambridge Univ. Press, Cambridge.

Côté, I. M. & Poulin, R., 1995. Parasitism and group size in social animals: a metaanalysis. *Behavioral Ecology*, 6: 159–165.

Davies, C. R., Ayres, J. M., Dye, C. & Deane, L. M., 1991. Malaria infection rate of Amazonian primates increases with body weight and group size. *Functional Ecology*, 5: 655–662.

DeWitt, T. J., 1997. Optimizing clutch size in birds. *Trends in Ecology and Evolution*, 12: 443.

Field, J., 1992. Intraspecific nest parasitism as an alternative reproductive tactic in nest–building wasps and bees. *Biological Reviews*, 67: 79–126.

Gladstone, D. E., 1979. Promiscuity in monogamous colonial birds. *American Naturalist*, 114: 545–557.

Grafen, A., 1988. On the uses of data on lifetime reproductive success. In: *Reproductive success: studies of individual variation in contrasting breeding systems*: 454–471 (T. H. Clutton–Brock, Ed.). Univ. of Chicago Press, Chicago.

Grenfell, B. T., Bjørnstad, O. N. & Kappey, J., 2001. Travelling waves and spatial hierarchies in measles epidemics. *Nature*, 414: 716–723.

Hamilton, W. D., 1964. The genetical evolution of social behavior. *Journal of Theoretical Biology*, 7: 1–52.

Hieber, C. S. & Uetz, G. W., 1990. Colony size and parasitoid load in two species of colonial *Metepeira* spiders from Mexico (Araneae: Araneidae). *Oecologia*, 82: 145–150.

Hoogland, J. L., 1995. *The black–tailed prairie dog: social life of a burrowing mammal*. University of Chicago Press, Chicago.

Jennions, M. D. & Petrie, M., 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews*, 75: 21–64.

Kempenaers, B., Verheyen, G. R., Van den Broeck, M., Burke, T., Van Broeckhoven, C. & Dhondt, A. A., 1992. Extra–pair paternity results from female preference for high quality males in the Blue Tit. *Nature*, 357: 494–496.

Kendall, W. L., 2004. Coping with unobservable and mis–classified states in capture–recapture studies. *Animal Biodiversity and Conservation,* 27.1: 97–107.

Kendall, W. L. & Nichols, J. D., 2002. Estimating state–transition probabilities for unobservable states using capture–recapture/resighting data. *Ecology*, 83: 3276–3284.

Klomp, H., 1970. The determination of clutch–size in birds: a review. *Ardea*, 58: 1–124.

Krasnov, B., Khokhlova, I. & Shenbrot, G., 2002. The effect of host density on ectoparasite distribution: an example of a rodent parasitized by fleas. *Ecology*, 83: 164–175.

Lack, D., 1947. The significance of clutch size. *Ibis*,

89: 302–352.

– 1954. *The natural regulation of animal numbers*. Clarendon Press, Oxford.

Lank, D. B., Rockwell, R. F. & Cooke, F., 1990. Frequency–dependent fitness consequences of intraspecific nest parasitism in Snow Geese. *Evolution*, 44: 1436–1453.

Lebreton, J. D. & Pradel, R., 2002. Multistate recapture models: modeling incomplete individual histories. *Journal of Applied Statistics*, 29: 353–369.

Lockhart, A. B., Thrall, P. H. & Antonovics, J., 1996. Sexually transmitted diseases in animals: ecological and evolutionary implications. *Biological Reviews*, 71: 415–471.

Loehle, C., 1995. Social barriers to pathogen transmission in wild animal populations. *Ecology*, 76: 326–335.

Lyon, B., 1993. Conspecific brood parasitism as a flexible female reproductive tactic in American Coots. *Animal Behaviour*, 46: 911–928.

Malmer, N. & Enckell, P. H., 1994. Ecological research at the beginning of the next century. *Oikos*, 71: 171–176.

Marshall, M. R., Diefenbach, D. R., Wood, L. A. & Cooper, R. J., 2004. Annual survival estimation of migratory songbirds confounded by incomplete breeding site–fidelity: life–history implications and study designs that may help. *Animal Biodiversity and Conservation*, 27.1: 59–72.

McRae, S. B. 1998. Relative reproductive success of female Moorhens using conditional strategies of brood parasitism and parental care. *Behavioral Ecology*, 9: 93–100.

Monath, T. P., Lazuick, J. S., Cropp, C. B., Rush, W. A., Calisher, C. H., Kinney, R. M., Trent, D. W., Kemp, G. E., Bowen, G. S. & Francy, D. B., 1980. Recovery of Tonate virus ("Bijou Bridge" strain), a member of the Venezuelan equine encephalomyelitis virus complex, from Cliff Swallow nest bugs (*Oeciacus vicarius*) and nestling birds in North America. *American Journal of Tropical Medicine and Hygiene*, 29: 969–983.

Moore, J., Simberloff, D. & Freehling, M., 1988. Relationships between Bobwhite quail social–group size and intestinal helminth parasitism. *American Naturalist*, 131: 22–32.

Mountford, M. D., 1973. The significance of clutch size. In: *The mathematical theory of the dynamics of biological populations*: 315–323 (M. S. Bartlett & R. W. Hiorns, Ed.). Academic Press, New York.

Nichols, J. D. & Kendall, W. L., 1995. The use of multi–state capture–recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics*, 22: 835–846.

Nisbet, I. C. T., 1989. Long–term ecological studies of seabirds. *Colonial Waterbirds*, 12: 143–147.

Payne, R. B., 1990. Natal dispersal, area effects, and effective population size. *Journal of Field Ornithology*, 61: 396–403.

Pradel, R., Hines, J. E., Lebreton, J.–D. & Nichols, J. D., 1997. Capture–recapture survival models taking account of transients. *Biometrics*, 53: 60–72.

Roff, D. A., 2002. *Life history evolution*. Sinauer, Sunderlund, Massachusetts.

Rohwer, F. C. & Freeman, S., 1989. The distribution of conspecific nest parasitism in birds. *Canadian Journal of Zoology*, 67: 239–253.

Rubenstein, D. I. & Hohmann, M. E., 1989. Parasites and social behavior of island feral horses. *Oikos*, 55: 312–320.

Sandell, M. I. & Diemer, M., 1999. Intraspecific brood parasitism: a strategy for floating females in the European Starling. *Animal Behaviour*, 57: 197–202.

Scott, T. W., Bowen, G. S. & Monath, T. P., 1984. A field study of the effects of Fort Morgan virus, an arbovirus transmitted by swallow bugs, on the reproductive success of Cliff Swallows and symbiotic House Sparrows in Morgan County, Colorado, 1976. *American Journal of Tropical Medicine and Hygiene*, 33: 981–991.

Sheldon, B. C., 1993. Sexually transmitted disease in birds: occurrence and evolutionary significance. *Philosophical Transactions of the Royal Society of London*, B 339: 491–497.

Stearns, S. C., 1992. *The evolution of life histories*. Oxford Univ. Press, Oxford.

Swinton, J., Harwood, J., Grenfell, B. T. & Gilligan, C. A., 1998. Persistence thresholds for phocine distemper virus infection in Harbour Seal *Phoca vitulina* metapopulations. *Journal of Animal Ecology*, 67: 54–68.

Tinkle, D. W., 1979. Long–term field studies. *Bioscience*, 29: 717.

VanderWerf, E., 1992. Lack's clutch size hypothesis: an examination of the evidence using meta–analysis. *Ecology*, 73: 1699–1705.

Wagner, R. H., 1993. The pursuit of extra–pair copulations by female birds: a new hypothesis of colony formation. *Journal of Theoretical Biology*, 163: 333–346.

Wagner, R. H., Schug, M. D. & Morton, E. S., 1996. Condition–dependent control of paternity by female Purple Martins: implications for coloniality. *Behavioral Ecology and Sociobiology*, 38: 379–389.

Weatherhead, P. J. & Boag, P. T., 1995. Pair and extra–pair mating success relative to male quality in Red–winged Blackbirds. *Behavioral Ecology and Sociobiology*, 37: 81–91.

Westneat, D. F., Sherman, P. W. & Morton, M. L., 1990. The ecology and evolution of extra–pair copulations in birds. *Current Ornithology*, 7: 331–369.

White, A., Begon, M. & Bowers, R. G., 1996. Host–pathogen systems in a spatially patchy environment. *Proceedings of the Royal Society of London* B, 263: 325–332.

White, G. C. & Burnham, K. P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46: S120–S139.

Yom–Tov, Y., 1980. Intraspecific nest parasitism in birds. *Biological Reviews*, 55: 93–108.

Yoshimura, J. & Shields, W. M., 1992. Components of uncertainty in clutch–size optimization. *Bulletin of Mathematical Biology*, 54: 445–464.