

A future cost of misdirected parental care for brood parasitic young?

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Abstract. Parental care is advantageous because it typically increases the survival of genetically related young. In contrast, parental care given to unrelated young incurs no benefit. A further cost of parental investment is that it reduces the future reproductive potential of the caregiver. I examined whether eastern phoebes' *Sayornis phoebe* future reproductive effort was related to interspecific brood parasitism by brown-headed cowbirds *Molothrus ater* in prior broods. In 2000 absolute and relative measures of change in clutch sizes from first to second breeding attempts were similar in parasitized and non-parasitized broods, while the latency to renest was several days shorter for parasitized broods. In addition, the relative change in clutch size was more negative for phoebe nests with more cowbird chicks per brood. In 2001 these statistical relationships between absolute and relative measures of residual effort and prior parasite load were also confirmed in control but not in experimentally manipulated clutches. The experimental data support previous findings that parasitism *per se* does not seem to influence residual reproductive output of adult phoebe hosts. These data also emphasize that intragenerational residual costs of parental care should be measured by the use of a relative measure of reproductive effort or other statistical methods that take into account the biological and statistical non-independence of clutch sizes from subsequent breeding attempts.

Key words: brood parasitism, clutch size, laying date, manipulation, parental care

Introduction

Parental care by hosts for nestlings of interspecific brood parasites is both genotypically and phenotypically costly because parasitic young use resources provided by foster parents without increasing the hosts' inclusive fitness (Davies 2000, Hauber & Dearborn 2003). Does interspecific brood parasitism have detrimental effects on adult hosts' residual or future reproductive effort (abbreviated hereafter as FRE)?

In some hosts of common cuckoos *Cuculus canorus* (Grim & Honza 1997, Kilner et al. 1999) and shining cuckoos *Chrysococcyx lucidus* (Gill 1982), parasitic chicks typically require no more feeding trips from the parents than a brood of host chicks (but see Grim & Honza 2001, Martin-Galvez et al. 2005 for different types of foods delivered to cuckoo chicks). Nonetheless, because cuckoo fledglings typically take longer to reach independence than host broods (Grim, in press), these parasites effectively reduce the chances for second brooding by foster parents.

A handful of published studies on few host species of brown-headed cowbirds *Molothrus ater* detected equivocal effects of parasitism status on adult reproduction, especially regarding parental feeding rates, between parasitized and non-parasitized broods (e.g., no overall difference: Hauber & Montenegro 2002, Kilpatrick 2002, Glassey & Forbes 2003; greater provisioning of parasitized broods: Dearborn et al. 1998, Hoover & Reetz 2006). In contrast, absolute measures of hosts' FRE when raising single cowbird chicks (e.g., decreased probabilities of second clutching,

seasonal and over-winter survival, or subsequent clutch sizes) were consistently similar between foster parents caring for parasitized vs. non-parasitized breeding attempts (Smith 1981, Payne & Payne 1998, Sedgewick & Iko 1999, Kus 2002, Hoover 2003a,b), despite the larger sizes and increased begging intensities of cohabiting parasite vs. host chicks (Dearborn 1998, Hauber 2003a). Yet, when brood size and parasite load were statistically accounted for, foster parents appeared to pay a cost of laying relatively fewer eggs after having raised broods with more parasitic cowbird young (Hauber 2002, Hoover & Reetz 2006). The difference between these alternative conclusions regarding the effect of parasitism on hosts' residual reproduction may be the use of absolute vs. relative measures of FRE.

Here I follow up on earlier findings (Hauber 2002) by comparing predictions of life history theory using both absolute and relative measures of FRE using additional data from unmanipulated and novel data from experimentally altered breeding attempts of eastern phoebes *Sayornis phoebe* parasitized by brown-headed cowbirds. Previous studies on non-parasitized phoebes demonstrated that increased current parental care for experimentally augmented conspecific broods had no effect on absolute measures of FRE (i.e. subsequent clutch size of individual females: Conrad & Robertson 1992). If greater parental investment were intragenerationally costly, I predicted that measures of FRE would be lower for larger broods and for broods with more parasites (i.e. higher parasite loads) because both of these factors are associated with increased parental care in current broods (Conrad & Robertson 1992, Hauber & Montenegro 2002). I also hypothesized that relative rather than absolute measures of FRE would more closely track prior levels of parental efforts because subsequent clutch sizes laid by the same females are not biologically independent (Kennedy & White 1991) and should be considered in statistical treatment of current vs. future reproductive data. I therefore examined an explicit assumption of this hypothesis, namely that there is statistical non-independence between individual phoebes' consecutive clutch sizes. Given that my analyses rest on several assumptions (see Methods), the study must be considered preliminary in its design but can be used to illustrate a methodological point of statistical interpretation of residual reproduction costs in hosts of brood parasites and of other iteroparous parental species (Clutton-Brock 1991, Stearns 1992).

Methods

Study species

Brown-headed cowbirds (hereafter: cowbirds) are widespread interspecific brood parasites in North America (Lother 1993). I studied intraseasonal breeding attempts (1–3, typically 2 / year) of a common cowbird host, the eastern phoebe (hereafter: phoebe), nesting on artificial substrates near Ithaca, NY, USA. At this site 37 % of first phoebe nesting attempts were parasitized ($n = 110$); for a more detailed description of the study site and general methods, see Hauber (2002).

Breeding parameters

I documented the progress of phoebe nesting attempts throughout the breeding seasons of 2000 and 2001. To control for potential confounding factors influencing hosts' site fidelity,

predator and human disturbances, and duration of parental care (H o o v e r 2003b), in the statistical analyses I included only those nests that successfully fledged at least one nestling (whether phoebe or cowbird) during the first breeding attempt. I approximated the clutch size for each breeding attempt by adding the total number of phoebe and cowbird eggs per clutch. This was done to account for host eggs removed by parasitic females (S e a l y 1994), averaging one host egg removed per each parasitic egg laid (L o w t h e r 1993, H a u b e r 2003a). I calculated clutch completion dates by monitoring clutch size during the laying period and assuming a rate of a single egg laid per day (for validation see H a u b e r & M o n t e n e g r o 2002, H a u b e r 2003b). For first nesting attempts I established brood sizes by adding the numbers of cowbird and phoebe chicks that survived to 5 days of age after their respective hatching dates (for justification, see H a u b e r 2003b). Parasite load was calculated as the number of cowbird chicks / brood size in that nest (H a u b e r 2002). I did not measure nestling mass and, thus, could not calculate brood weights and parasitism load relative to total brood mass (H o o v e r 2003a, H o o v e r & R e e t z 2006).

Although phoebes in this study were not marked for individual identification, I assumed that in a given year all consecutive breeding attempts in or near a nest (i.e., on the same building or under the same bridge) could be consistently attributed the same breeding pair because phoebes are territorial and socially monogamous, and reuse nests multiple times per year (K l a s 1975), and because at another site individually marked phoebe pairs stayed together and bred on the same territory during the same summer in over 85% of monitored cases (B e h e l e r et al. 2003). For second nests I again established clutch completion dates and sizes, and calculated the difference in days between dates of second and first clutch completion dates to quantify the latency to renest.

Both the observational and experimental data included in this study come from a separate set of breeding attempts from those published in H a u b e r (2002). All data from 2000 were obtained from nests observed without manipulating clutch content. In 2001, phoebe breeding attempts were used as part of a clutch manipulation experiment (H a u b e r 2003b). In that experiment I altered the content of a haphazardly chosen subset of nests in one of two ways. For the purposes of this report, (1) *control nests* had one phoebe or cowbird egg removed and replaced by a similar-stage phoebe or cowbird egg, respectively, from a different nest (i.e., the predicted clutch completion dates were ≤ 1 day different between the two nests); (2) *experimental nests* had one phoebe or cowbird egg removed and replaced with a phoebe or cowbird egg whose predicted hatching dates were 5 or more days before or after that of the removed egg. The manipulation had the effect of altering brood sizes from what was predicted given the clutch size and the number of cowbird eggs in the original clutch (H a u b e r 2003b,c). These manipulations allowed both for comparing observational data from this and the previous study (H a u b e r 2002) in the context of different parasite loads and disentangling the effect of unmeasured potentially confounding variables from the predictor variables of clutch size, brood size, and parasite load.

The size of the second clutches served as an absolute measure of FRE (aFRE). As a relative measure of FRE (rFRE) I calculated the standardized difference between first and second clutch sizes as $[2^{\text{nd}} - 1^{\text{st}} \text{ clutch sizes}] / 1^{\text{st}} \text{ clutch size}$ (following H a u b e r 2002). From a statistical perspective it is important to note that if all phoebes laid a clutch size consisting of one less egg in the second breeding attempt than in first breeding attempt irrespective of parasitism, in the context of my measure of aFRE this would produce a correlation with a positive rather than a zero slope between second clutch sizes and first brood sizes given a strong relationship between first clutch size and brood size. Similarly,

the same pattern of laying one egg less in second clutches irrespective of parasitism would lead to a positive correlation between rFRE. In the absence of directional predictions, all statistical tests were two-tailed and mean \pm SE values are shown.

Results

In 2000 the data from the non-manipulated eastern phoebe nests showed a positive, statistical relationship between clutch sizes of first and second breeding attempts at the same nest site (Spearman's rank correlation: $r_s = 0.37$, $Z = 2.0$, $P = 0.049$, $N = 28$). There was no difference in the estimated host clutch sizes of first breeding attempts at parasitized and non-parasitized sites: total number of eggs per nest were 5.3 ± 0.31 eggs, and 4.9 ± 0.18 eggs, respectively: $t_{30} = -1.2$, $P = 0.24$). The latency to renest was on average 4.5 days shorter following broods parasitized by brown-headed cowbirds vs. non-parasitized broods (39.1 ± 1.2 days vs. 43.6 ± 1.3 days, respectively, $t_{23} = 2.4$, $P = 0.023$).

The absolute and relative measures of FRE were respectively similar in magnitude between parasitized and non-parasitized nest sites in 2000. Hosts' second clutch sizes, or aFRE values, were 4.3 ± 0.22 eggs at parasitized nests and 4.4 ± 0.11 eggs at non-parasitized nests ($t_{30} = 0.68$, $P = 0.50$); rFRE values were also similar: -0.059 ± 0.027 for parasitized nests and -0.033 ± 0.021 for non-parasitized nests ($t_{27} = 0.73$, $P = 0.47$). In addition, in multiple regression analyses rFRE, but not aFRE values, were significantly and negatively related to the brood sizes and parasite loads during the first breeding attempts (aFRE: $R^2 = 0.048$, $P = 0.54$; rFRE = $0.18 - 0.048 \times 1^{\text{st}} \text{ Brood Size} - 0.53 \times 1^{\text{st}} \text{ Parasite Load}$, $R^2 = 0.29$, $P = 0.014$; log-transformed rFRE: $R^2 = 0.22$, $P = 0.016$).

In 2001, the proportions of parasitized nests were similar between control (5 of 15) and experimental (10 of 19) clutches ($P = 0.31$, Fisher's exact test). There was a negative statistical relationship between first and second clutch sizes at control nest sites ($r_s = -0.67$, $Z = -2.5$, $P = 0.012$) but not at experimental nest sites ($r_s = 0.018$, $Z = 0.077$, $P = 0.94$). As in 2000, there was no significant difference between parasitized/asynchronous and non-parasitized broods regarding aFRE or rFRE for either control or experimental clutches (all $P > 0.2$, Fig. 1A-C). In multiple regression analyses both aFRE and rFRE were negatively related to both brood size and parasite load in first clutches at control sites (aFRE = $8.4 - 0.81 \times 1^{\text{st}} \text{ Brood Size} - 4.4 \times 1^{\text{st}} \text{ Parasite Load}$, $R^2 = 0.48$, $P = 0.019$, Fig. 1A; rFRE = $1.4 - 0.30 \times 1^{\text{st}} \text{ Brood Size} - 1.4 \times 1^{\text{st}} \text{ Parasite Load}$, $R^2 = 0.33$, $P = 0.088$, Fig. 1B; for log-transformed rFRE $R^2 = 0.49$, $P = 0.02$) (Fig. 1). These patterns were not statistically significant for experimental sites (aFRE $R^2 = 0.09$, $P = 0.48$, rFRE: $R^2 = 0.12$, $P = 0.37$, Fig. 1C).

Discussion

Observational and experimental data from this study (Fig. 1A-C) provide further support for the finding that eastern phoebes pay consistently disproportionately greater costs for raising a parasitic brown-headed cowbird nestling when compared to raising one of their own offspring (Kilpatrick 2002, Hauber 2002, Kilner et al. 2004). However, parasitized phoebes also raise fewer total nestlings per brood than do non-parasitized conspecifics (Klaas 1975, Hauber & Montenegro 2002, Hauber 2003a), and have shorter latencies of about 4 days to renest (this study). Perhaps as a combined result of these opposing correlates of parasitism, cowbird parasitism *per se* is not statistically related to subsequent clutch sizes as absolute or relative measures future reproductive effort in eastern phoebes.

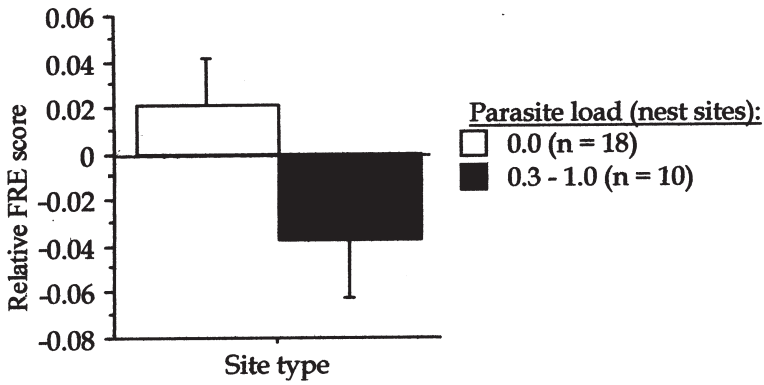


Fig. 1A

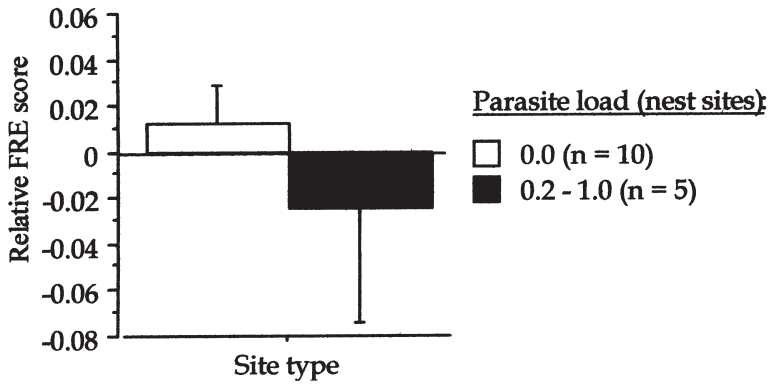


Fig. 1B

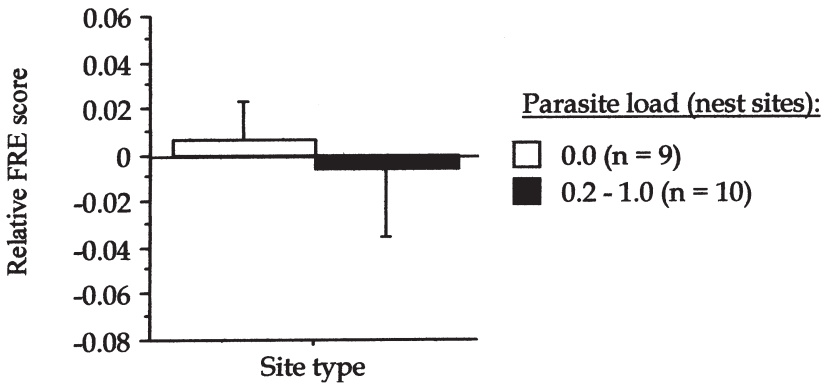


Fig. 1C

Fig. 1. The relationship between relative change from first to second clutch sizes (rFRE) and parasite loads of first breeding attempts in A: 2000 (control), B: 2001 (control), and C: 2001 (experimental). Residual values are plotted for $\log(x+1)$ transformed rFRE values from a regression analysis with brood size of first breeding attempts; mean \pm SE.

These findings are in concert with those for the few other passerine hosts of cowbirds in North America for which similar data on residual reproductive success are known (Smith 1981, Arcese et al. 1996, Payne & Payne 1998, Kus 2002). Whether cowbird parasitism influences other aspects of the future fitness of phoebe foster parents, especially

regarding return rates, dispersal, and reproductive behaviors during subsequent years (Payne & Payne 1998, Hoover 2003a, Hoover & Reetz 2006), remains to be elucidated. Nonetheless, current evidence indicates that cowbird parasitism consistently reduces the survival and recruitment of some of the offspring in parasitized broods while the affect of parasitism on reducing adult hosts' absolute residual fitness remains less predictable. Such differences of the impact of brood parasitism on hosts' breeding effort have important implications for the co-evolution of host life history traits and parasitic virulence (Hauber 2003d, Kilner 2005, Rasmussen & Sealy 2006, Servedio & Hauber 2006).

These analyses may have relevance to life history trait studies beyond host-parasite interactions regarding the comparison of absolute and relative measures of future reproductive effort (FRE). Current and future reproductive efforts of the same individual or breeding pairs are biologically non-independent (Chastel & Kersten 2002) and statistical tests designed to examine the effect of parental care on future reproductive effort should take into consideration this potential statistical confound as a possible source of unaccounted variability. Earlier studies that examined absolute values of offspring numbers following differential parental care did not always adhere to this requisite and only rarely detected a causal relationship between increased brood size and absolute measured of residual or future reproductive effort (reviewed by Murphy 2000).

In support of a need of revised analytical approaches in the study of FRE with a focus on individuals, I found that clutch sizes from consecutive breeding attempts of eastern phoebes were statistically related in the first, observational year (2000) of this study. In the second, experimental year (2001) a statistical relationship in the opposite direction was found, and only in nests where brood content had not altered from its original size and content. Why the signs of these relationships were not consistent (positive correlation in 2000, negative correlation in 2001) remains to be studied further. Yet, the consistent patterns of statistical non-independence between subsequent clutch sizes in phoebes and other passerine birds (Kennedy & White 1991, Gwinner et al. 1995; Banbura & Zielinski 2000, Christians et al. 2001, Robertson & Rendell 2001) justify the methodological premise of this study that led to the comparison of absolute and relative measures of FRE following cowbird parasitism. Indeed, only relative measures of FRE were consistently lower for larger brood sizes and greater parasite loads in unmanipulated and control phoebe nests (Hauber 2002).

It appears that rearing brood parasitic young is more costly on a per-chick basis, perhaps because cowbirds both require and are fed disproportionately more food than phoebe chicks (Hauber & Montenegro 2002, Kilner et al. 2004), as was found in other parasitic systems as well (Grim & Honza 2001). Yet, surprisingly, brown-headed cowbird parasitism *per se* does not reduce future reproductive effort by eastern phoebes. This may be caused by parasites that preferentially lay into nests of high quality host individuals (Smith 1981, Hauber 2001). These comparisons also imply that intragenerational residual costs of parental care should be evaluated by statistical methods that take into account the biological non-independence of clutch sizes from subsequent reproductive attempts by individual breeders.

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LITERATURE

- Arcese P., Smith J.N.M. & Hatch J.I. 1996: Nest predation by cowbirds, and its consequences for passerine demography. *Proceedings of the National Academy of Sciences USA* 93: 4608–4611.
- Banbura J. & Zielinski P. 2000: Repeatability of reproductive traits in female barn swallows *Hirundo rustica*. *Ardea* 88:75–80.
- Beheler A.S., Rhodes O.E. Jr. & Weeks H.P. Jr. 2003: Breeding site and mate fidelity in Eastern Phoebes (*Sayornis phoebe*) in Indiana. *Auk* 120: 990–999.
- Chastel O. & Kersten M. 2002: Brood size and body condition in the House Sparrow *Passer domesticus*: the influence of brood behaviour. *Ibis* 144: 284–292.
- Christians J.K., Evanson M. & Aiken J.J. 2001: Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. *J. Anim. Ecol.* 70: 1080–1087.
- Conrad K.F. & Robertson R.J. 1992: Intraseasonal effects of clutch manipulation on parental provisioning and residual reproductive value of Eastern phoebes (*Sayornis phoebe*). *Oecologia* 89: 356–364.
- Clutton-Brock T.H. 1991: The Evolution of Parental Care. *Princeton University Press, Princeton, NJ, USA*.
- Davies N.B. 2000: Cuckoos, Cowbirds and Other Cheats. *T & AD Poyser, London, UK*.
- Dearborn D.C. 1998: Begging behavior and food acquisition by brown-headed cowbird nestlings. *Behav. Ecol. Sociobiol.* 43: 259–270.
- Dearborn D.C., Anders A.D., Thompson F.R. III. & Faaborg J. 1998: Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. *Condor* 100: 326–334.
- Gil B.J. 1982: The Grey Warbler's care of nestlings: A comparison between unparasitized broods and those comprising a Shining Bronze-Cuckoo. *Emu* 82: 177–181.
- Glasse B. & Forbes S. 2003: Why brown-headed cowbirds do not influence red-winged blackbird parent behaviour. *Anim. Behav.* 65: 1235–1246.
- Grim T. & Honza M. 1997: Differences in parental care of reed warbler (*Acrocephalus scirpaceus*) in its own nestlings and parasitic cuckoo (*Cuculus canorus*) chicks. *Folia Zool.* 46: 135–142.
- Grim T. & Honza M. 2001: Does supernormal stimulus influence parental behaviour of the cuckoo's host? *Behav. Ecol. Sociobiol.* 49: 322–329.
- Grim T., in press: Experimental evidence for chick discrimination without recognition in a brood parasite host. *Proceedings of the Royal Society of London B*.
- Gwinner E., Konig S. & Haley C.S. 1995: Genetic and environmental factors influencing clutch size in equatorial and temperate zone stonechats (*Saxicola torquata axillaris* and *S. t. rubicola*): an experimental study. *Auk* 112: 748–755.
- Hauber M.E. 2001: Site selection and repeatability in Brown-Headed Cowbird (*Molothrus ater*) parasitism of Eastern Phoebe (*Sayornis phoebe*) nests. *Can. J. Zool.* 79: 1518–1523.
- Hauber M.E. 2002: Is reduced clutch size a cost of parental care in Eastern Phoebes (*Sayornis phoebe*)? *Behav. Ecol. Sociobiol.* 51: 503–509.
- Hauber M.E. 2003a: Lower begging responsiveness of host vs. cowbird nestlings is related to species identity but not to early social experience in parasitized broods. *J. Comp. Psych.* 117: 24–30.
- Hauber M.E. 2003b: Hatching asynchrony, nestling competition, and the cost of interspecific brood parasitism. *Behav. Ecol.* 14: 224–235.
- Hauber M.E. 2003c: Egg-capping is a cost paid by hosts of interspecific brood parasites. *Auk* 120: 860–865.
- Hauber M.E. 2003d: Interspecific brood parasitism and the evolution of host clutch sizes. *Evol. Ecol. Res.* 5: 559–570.
- Hauber M.E. & Montenegro K. 2002: What are the costs of raising a brood parasite? Comparisons of host parental care at parasitized and non-parasitized broods. *Etologia* 10: 1–9.

- Hauber M.E. & Dearborn D.C. 2003: Parentage without parental care: what to look for in genetic studies of obligate brood-parasitic mating systems. *Auk* 120: 1–13.
- Hoover J.P. 2003a: Multiple effects of brood parasitism reduce the reproductive success of prothonotary warblers, *Protonotaria citrea*. *Anim. Behav.* 65:923–934.
- Hoover J.P. 2003b: Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* 84: 416–430.
- Hoover J.P. & Reetz M.J. 2006: Brood parasitism increases provisioning rate and reduces offspring recruitment and adult return rates in a cowbird host. *Oecologia* 149: 165–173.
- Kennedy E.D. & White D.W. 1991: Repeatability of clutch size in house wrens. *Wilson Bulletin* 103: 552–558.
- Kilpatrick A.M. 2002: Variation in growth of Brown-headed Cowbird (*Molothrus ater*) nestlings and energetic impacts on their host parents. *Can. J. Zool.* 80: 145–153.
- Kilner R.M. 2005: The evolution of virulence in brood parasites. *Ornithological Science* 4: 55–64.
- Kilner R.M., Noble D.G. & Davies N.B. 1999: Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature* 397: 667–672.
- Kilner R.M., Madden J. & Hauber M.E. 2004: Brood parasitic cowbird nestlings use host young to procure parental resources. *Science* 305: 877–879.
- Klaas E.E. 1975: Cowbird parasitism and nesting success in the Eastern Phoebe. *Occasional Papers of the Kansas Museum of Natural History* 41: 1–18.
- Kus B.E. 2002: Fitness consequences of nest desertion in an endangered host, the Least Bells' Vireo. *Condor* 104: 795–802.
- Lowther P.E. 1993: Brown-headed Cowbird (*Molothrus ater*). In: Poole A. & Gill F. (eds), *The Birds of North America*, No. 47. *The Academy of Natural Sciences, Philadelphia*.
- Martin-Galvez D., Soler M., Soler J.J., Martin-Vivaldi M. & Palomino J.J. 2005: Food acquisition by common cuckoo chicks in rufous bush robin nests and the advantage of eviction behaviour. *Anim. Behav.* 70: 1313–1321.
- Murphy M.T. 2000: Evolution of clutch size in the eastern kingbird: tests of alternative hypotheses. *Ecological Monographs* 70: 1–20.
- Payne R.B. & Payne L.L. 1998: Brood parasitism by cowbirds: risks and effects on reproductive success and survival in indigo buntings. *Behav. Ecol.* 9: 64–73.
- Rasmussen J.L. & Sealy S.G. 2006: Hosts feeding only Brown-headed Cowbird fledglings: where are the host fledglings? *J. Field Ornithol.* 77: 269–279.
- Robertson R.J. & Rendell W.B.. 2001: A long-term study of reproductive performance in tree swallows: the influence of age and senescence on output. *J. Anim. Ecol.* 70: 1014–1031.
- Sealy S.G. 1994: Observed acts of egg destruction, egg removal, and predation on nests of passerine birds at Delta Marsh, Manitoba. *Canadian Field Naturalist* 108: 41–51.
- Sedgewick J.A. & Iko W.M. 1999: Costs of Brown-headed Cowbird parasitism to Willow Flycatchers. *Studies in Avian Biology* 18: 167–181.
- Servedio M. & Hauber M.E. 2006: To eject or to abandon? Brood parasite virulence and host clutch sizes interact to influence the fitness payoffs of alternative rejection strategies. *J. Evol. Biol.* 19: 1585–1594.
- Smith J.N.M. 1981: Cowbird parasitism, host fitness, and age of the host female in an island Song Sparrow population. *Condor* 83: 152–161.
- Stearns S.C. 1992: *The Evolution of Life Histories*. Oxford University Press, New York, USA.