

Parasites favour intermediate nestling mass and brood size in cliff swallows

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Abstract

A challenge of life-history theory is to explain why animal body size does not continue to increase, given various advantages of larger size. In birds, body size of nestlings and the number of nestlings produced (brood size) have occasionally been shown to be constrained by higher predation on larger nestlings and those from larger broods. Parasites also are known to have strong effects on life-history traits in birds, but whether parasitism can be a driver for stabilizing selection on nestling body size or brood size is unknown. We studied patterns of first-year survival in cliff swallows (*Petrochelidon pyrrhonota*) in western Nebraska in relation to brood size and nestling body mass in nests under natural conditions and in those in which hematophagous ectoparasites had been removed by fumigation. Birds from parasitized nests showed highest first-year survival at the most common, intermediate brood-size and nestling-mass categories, but cliff swallows from nonparasitized nests had highest survival at the heaviest nestling masses and no relationship with brood size. A survival analysis suggested stabilizing selection on brood size and nestling mass in the presence (but not in the absence) of parasites. Parasites apparently favour intermediate offspring size and number in cliff swallows and produce the observed distributions of these traits, although the mechanisms are unclear. Our results emphasize the importance of parasites in life-history evolution.

Introduction

A current challenge in evolutionary biology is to explain why organisms do not keep getting bigger (Blanckenhorn, 2000; Bonnet *et al.*, 2017). Larger size has often been shown to be advantageous in a variety of ways: for example, heavier nestling passerine birds often survive better, at least in the short term, than their lighter counterparts (e.g. Krementz *et al.*, 1989; Monrós *et al.*, 2002; Schwagmeyer & Mock, 2008; Medeiros & Freed, 2009; Cleasby *et al.*, 2010; Bouwhuis *et al.*, 2014). Given moderate levels of heritability for nestling mass in some species (van Noordwijk *et al.*, 1980, 1988; Charmantier *et al.*, 2004a; Garant *et al.*, 2004), directional selection should favour the larger

offspring and the parents producing them. What, then, constrains continued increases in average nestling mass (Blanckenhorn, 2000; Clegg *et al.*, 2008; Gotanda *et al.*, 2015; Rollinson & Rowe, 2015; Bonnet *et al.*, 2017)?

In the case of nestling birds, the best evidence for a disadvantage of larger size comes from a relatively few studies that have shown higher post-fledging predation rates on heavier nestlings (Tinbergen & Boerlijst, 1990; Lindén *et al.*, 1992; Adriaensen *et al.*, 1998; Covas *et al.*, 2002; Gow & Wiebe, 2014), presumably because relatively heavy birds are less agile in flight and easier for avian predators to catch and kill (Lind *et al.*, 2010). A long-term study showed changes in the relationship between fledgling mass and survival in years when avian predators were present vs. absent (Bouwhuis *et al.*, 2014). A related study showed that fledglings from larger broods were hungrier and for this reason more conspicuous and more likely to be taken by hawks (Götmark, 2002). These results suggest that predation drives stabilizing selection on both nestling mass

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and brood size and that predation, in part, constrains directional selection for larger body size or brood size.

Another potential influence on body and brood size is parasitism. Many studies, for example, have measured the effects of ectoparasites on nestling mass or survival, some finding that both decline among more heavily parasitized offspring (Moss & Camin, 1970; Brown & Brown, 1986; Norris *et al.*, 2010; reviewed in Brown & Brown, 2001). This work has led to the tacit assumption that in species subject to heavy parasitism, bigger (or heavier) nestlings can better buffer the cost of parasitism and thus should be favoured through higher survival. However, evidence is now accumulating that ectoparasites may sometimes preferentially feed on the heavier nestlings within broods (Roulin *et al.*, 2003; Valera *et al.*, 2004; Bize *et al.*, 2008) and that larger individuals may also present a greater target area, making them easier for parasites to locate (Mohr, 1961; Port & Boreham, 1980; Cable & van Oosterhout, 2007) and attracting more as a result. Smaller brood sizes may increase per capita extent of parasitism (Richner & Heeb, 1995), whereas larger brood sizes may lead to nestlings being immunologically compromised (Hörak *et al.*, 1999; Saino *et al.*, 2002). The result could be that the presence of parasites might favour nestlings of intermediate weight and those in intermediate-sized broods. To date, no study to our knowledge has examined whether ectoparasites might drive stabilizing selection on body mass or brood size in birds.

In this study, we examine whether nestling cliff swallows (*Petrochelidon pyrrhonota*) of certain masses and brood sizes have survival costs or benefits and thus whether there is evidence for stabilizing selection around an intermediate optimum in each case. By comparing birds at sites where parasites had been experimentally removed by fumigation to individuals raised under natural levels of parasitism, we investigate whether blood-sucking cimicid bugs favour birds of intermediate body masses and/or brood sizes. The results offer insight into a previously unrecognized mechanism that may drive stabilizing selection on nestling mass and brood size.

Materials and methods

Study animal and study site

The cliff swallow is a migratory, sparrow-sized passerine bird found throughout the Great Plains and westward to the Pacific coast of North America; smaller populations exist in the eastern half of the continent (Brown *et al.*, 2017). Historically, these birds built their gourd-shaped mud nests underneath horizontal overhangs on the sides of steep cliffs, often in high density, although now many cliff swallows nest under the sides of bridges and buildings or inside concrete culverts underneath roads or railways (Brown *et al.*, 2013). The birds arrive

in our study area beginning in late April, and most colonies have completed nesting by late July. The species winters in southern South America, primarily Argentina (Brown *et al.*, 2017).

We studied cliff swallows near the Cedar Point Biological Station (41.2097°N, 101.6480°W) in southwestern Nebraska along the North and South Platte rivers, with the study area including portions of Keith, Deuel, Garden, Lincoln and Morrill counties. In this area, the birds nest mostly on the sides of bridges and in box-shaped road culverts (Brown *et al.*, 2013). Colonies were defined as birds from groups of nests that interacted at least occasionally in defence against predators or by sharing information on the whereabouts of food. Typically, all the nests on a given bridge or road culvert constituted a colony (Brown & Brown, 1996), with most colonies separated from the next nearest one by 1–10 km. Colony size varied widely; in our study area, it ranged from 2 to 6000 nests (mean \pm SE, 404 ± 13 , $n = 2318$ colonies), with some birds nesting solitarily.

Field methods

At 60 total colonies, 1982–1989, we monitored cliff swallow nests through bi-daily nest checks (using a flashlight and dental mirror inserted through each nest's mud entrance), enabling us to know the hatching date of each clutch and thus the subsequent age of all nestlings. Nestling cliff swallows in those colonies were banded with uniquely numbered US Geological Survey bands at 10 days of age (Brown & Brown, 1986), and at that time were weighed to the nearest 0.5 g using a Pesola scale. Any ectoparasite (swallow bugs and fleas) visible on a nestling was counted (Brown & Brown, 1996). Mass taken at 10 days, near the time when nestlings attain maximum weight, strongly predicted mass at fledging (C. R. Brown, unpubl. data). Sex could not be determined for nestling cliff swallows. Brood size was the number of nestlings present at 10 days.

We monitored the annual survival of the nestlings from 1982 to 1989 via systematic mist-netting of adults at 12–40 colony sites each season from 1983 to 2013 (Brown, 1998; Brown & Brown, 2004a; Roche *et al.*, 2013). No birds from the 1982 to 1989 cohorts were captured after 1998, and thus, all had presumably completed their lifespan by then. Birds were captured by putting nets across the entrances of highway culverts or along the sides of bridges that contained swallow colonies. Swallows were caught as they exited their nests. At a few select colonies, we captured adults inside their nests at night for parentage studies (Brown & Brown, 1988). We rotated among the accessible colonies, netting at each several times each season.

Some colony sites in the study area were fumigated in part or in whole each year to remove ectoparasitic swallow bugs (Hemiptera: Cimicidae: *Oeciacus vicarius*; Brown & Brown, 1986, 1996, 2004b). Swallow bugs

are the major nest parasite of cliff swallows. Nests were lightly sprayed with a dilute solution of Dibrom, an organophosphate insecticide that is highly effective against swallow bugs (Brown & Brown, 2004b; Runjaic *et al.*, 2017). Fumigated nests were not completely parasite-free, as bugs were occasionally transported into nests by transient birds (Brown & Brown, 2004b; Moore & Brown, 2014). However, the parasite load in fumigated nests remained much lower: for example, the mean number of bugs per fumigated nest at one site (depending on date) varied from 0.09 to 0.24, compared to 7.53–150.49 bugs per nonfumigated nest at the same site (Runjaic *et al.*, 2017). In the present study, 99.4% of nestlings from fumigated nests had a count of 0 swallow bugs at 10 days of age, compared to 76.9% of nestlings from nonfumigated nests. Given how few bugs were found in fumigated nests, bug parasitism was disregarded in all analyses involving nestlings from fumigated nests. The fleas (Siphonaptera: Ceratophyllidae: *Ceratophyllus celsus*) infesting cliff swallow nests seemed unaffected by nest fumigation (Brown & Brown, 1996), and thus, fleas were included in analyses involving fumigated nests.

Fumigation began as birds were settling at a site (during nest-building) and continued at 7- to 10-day intervals throughout the nesting season (until all nestlings had fledged). Fumigation occurred at seven colonies in 1984, eight in 1985, three in 1986, three in 1987, three in 1988 and one in 1989. These colonies were either divided such that one-half of the nests at the site received fumigation and the other half did not (13 colonies), or were fumigated in their entirety in a given year (12 colonies). The remaining 35 colonies from 1982 to 1989 had no fumigation. Sample sizes were 3010 nestlings from 986 nonfumigated nests (with insufficient data [$n = 12$ nestlings] to estimate survival in 1985) and 7248 nestlings from 2370 fumigated nests.

Colony size in all cases refers to the maximum number of active nests at a site, with an active nest defined as one in which one or more eggs were laid. Colony sizes were determined by direct counts of all active nests (from inspecting nest contents) or by estimation based both on nest counts of portions of a colony site and on the number of birds present at a site (Brown & Brown, 1996; Brown *et al.*, 2013). Colony sizes in this study varied from 1 to 1600 nests for nonfumigated colonies and 1 to 2200 nests for fumigated colonies.

Estimating annual survival

Survival of birds banded as nestlings to the next (their first) breeding season was considered first-year survival. As in any mark–recapture study of an open population (Lebreton *et al.*, 1992), our analyses measured local apparent survival only; permanent emigration from the study area was confounded with mortality. We make the assumption here that nestling mass and brood size

did not influence permanent emigration in ways that would lead to biased survival estimates for individuals from different parts of each trait's distribution.

Capture histories, indicating in what years a bird was first banded and later recaptured, were constructed for all individuals in the 1982–1989 cohorts. These capture histories were used in program MARK (White & Burnham, 1999) to generate maximum-likelihood Cormack–Jolly–Seber recaptures-only annual survival estimates. An age-based model structure for survival (age 1, all others combined) was used because we were specifically interested in first-year survival and because first-year survival is known to differ from that of older age classes in cliff swallows (Brown & Brown, 1996; Brown *et al.*, 2015, 2016). The same age-based model structure was used for recapture probability, given other analyses showing this model structure was best for nestling cliff swallows (Brown *et al.*, 2016). Both survival and recapture probabilities were modelled as fully time-dependent (i.e. survival and recapture estimated for each year separately).

For first-year survival, the variables of hatching date, brood size, nestling mass, number of fleas per bird and number of swallow bugs per bird were modelled as continuous linear covariates. We did not include clutch size because it was strongly associated with brood size. All models also contained colony size as a continuous covariate, as we had found effects of colony size on first-year survival using a much larger data set (Brown *et al.*, 2016). We fit combinations of the relevant linear (and quadratic) covariates to both survival and recapture to ascertain which mark–recapture model(s) best described the variation in our data. All covariates were standardized within each year to yield a mean of 0 and a standard deviation of 1.

Overdispersion in the mark–recapture data was addressed by calculating a median c -hat in MARK ($\hat{c} = 1.54$) for the fully parameterized Cormack–Jolly–Seber model (without covariates) and using that c -hat to adjust parameter variances and infer model fit (resulting in QAIC_c). The highest ranking (best-fitting) model was determined to be the one with the lowest QAIC_c value (Burnham & Anderson, 2002), and any with a $\Delta\text{QAIC}_c \geq 2$ to have limited support from the data.

Statistical analyses

Analyses that employed mixed models treated (in all cases) nest identity nested within colony site as a random effect. This was done to control for the likelihood that variables such as nestling mass, brood size or parasite load may not have been statistically independent among the birds from a given nest and a given colony site. We used Proc MIXED in SAS to do multiple regression or analyses of covariance (ANCOVA). Our approach was to begin with a global model containing all

(model 1; Table 1) for both brood size and nestling mass were negative and significantly different from 0 (Table 3a). There was a significant negative effect of swallow bugs on survival, and the effect of colony size varied among years (Table 3a). Estimated survival probabilities for birds from nonfumigated nests in relation to brood size (Fig. 1) and nestling mass (Fig. 2) for four years (with the largest sample sizes) revealed peak survival matching generally the modal brood-size and nestling-mass categories. Results for other years were similar to those shown in Figs 1 and 2.

The top model for first-year survival of birds from fumigated nests included linear effects of brood size, hatching date, nestling mass, colony size and number of fleas, with all but colony size using the same function across years (model 1; Table 2). Thus, only the effect of colony size varied among years. There was little evidence for survival peaking at intermediate values of brood size or nestling mass for birds from fumigated nests, given that models with quadratic functions for these variables (e.g. models 2–6; Table 2) had QAIC_c values > 2 higher than the top model (Table 2). No other interaction terms

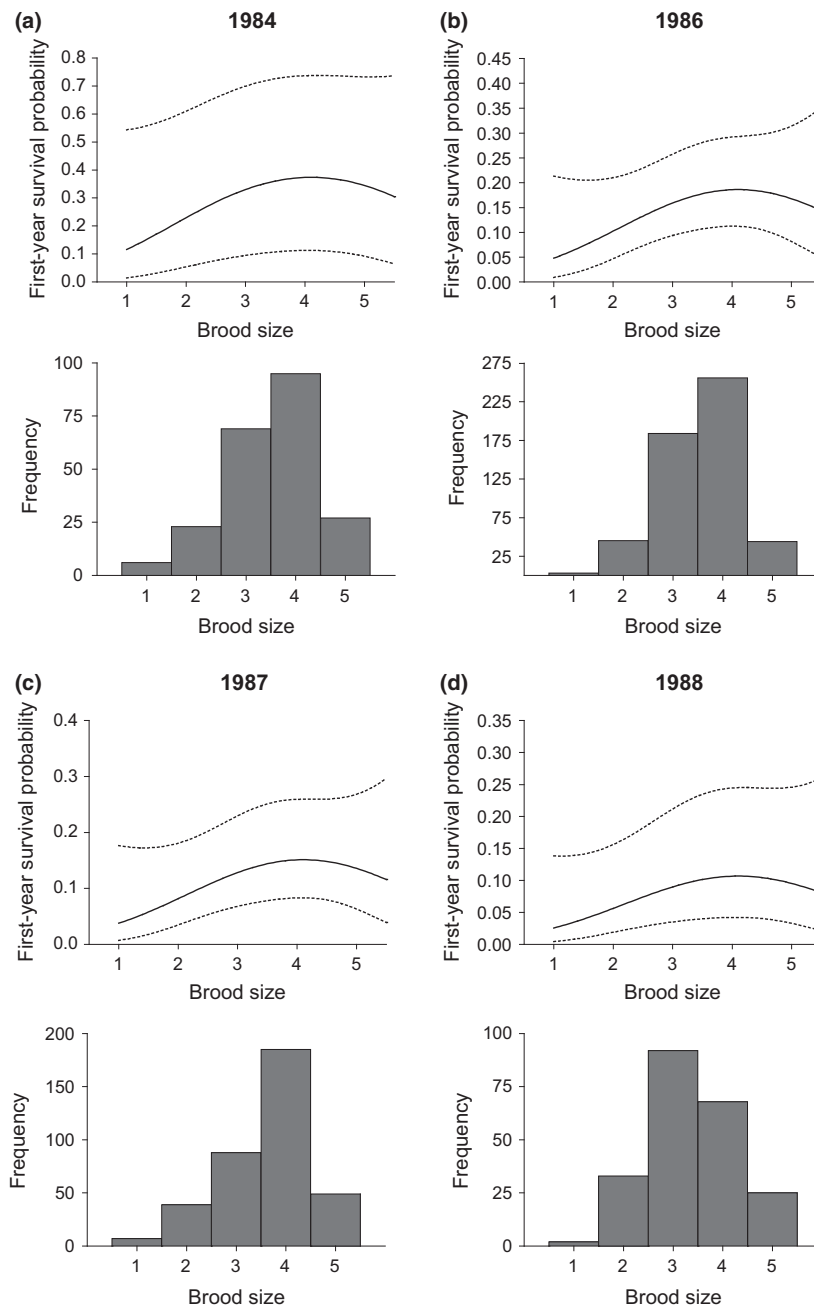


Fig. 1 Estimated first-year survival probabilities for cliff swallows from nonfumigated nests in relation to brood size, and the observed frequencies of brood sizes, in four representative years (a–d). Survival was estimated from the top model (model 1, Table 1), and curves shown were solved at mean values of all other covariates. Predicted survival is indicated with a solid line, and dotted lines show 95% confidence limits.

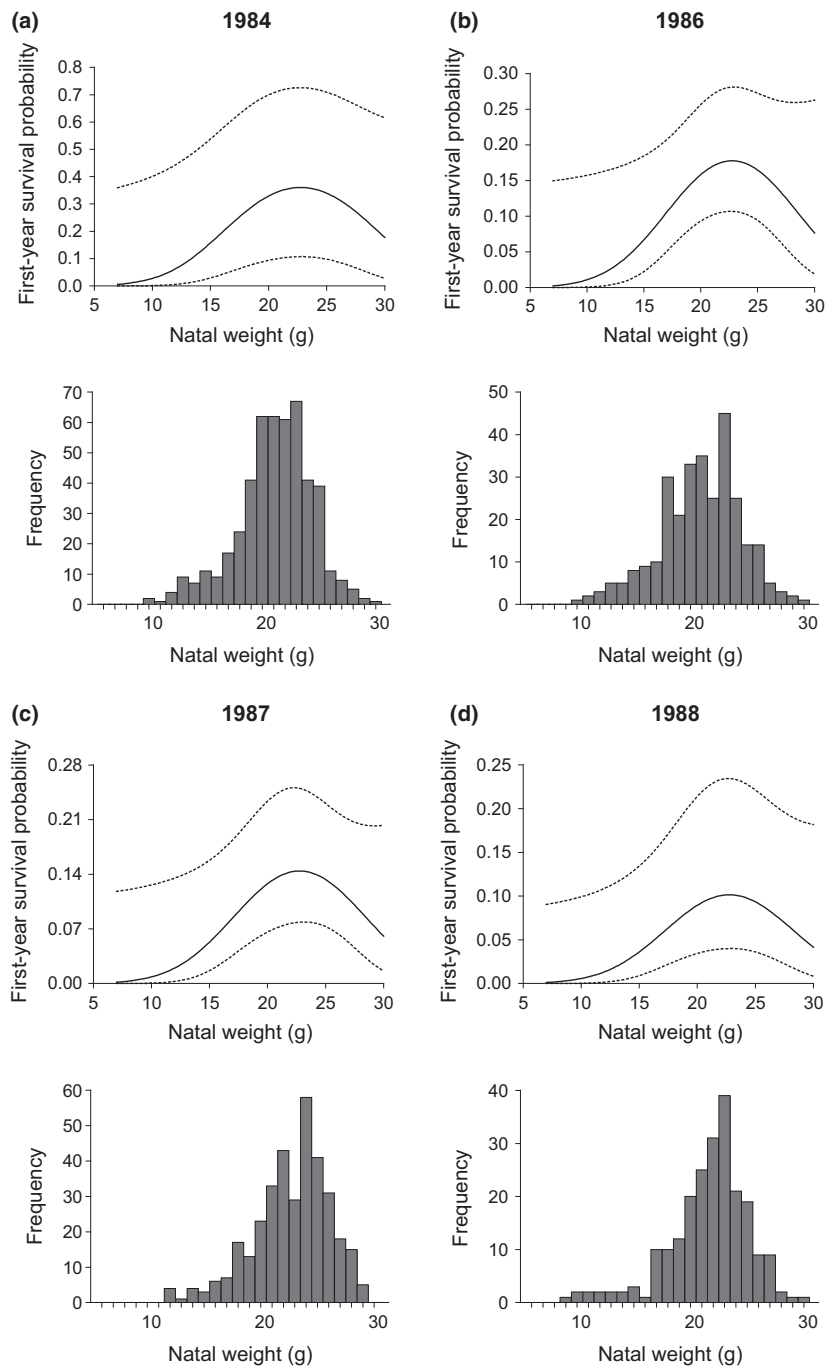


Fig. 2 Estimated first-year survival probabilities for cliff swallows from nonfumigated nests in relation to nestling mass (in g), and the observed frequencies of nestling mass categories, in four representative years (a–d). Survival was estimated from the top model (model 1, Table 1), and curves shown were solved at mean values of all other covariates. Predicted survival is indicated with a solid line, and dotted lines show 95% confidence limits.

had support ($\Delta\text{QAIC}_c > 15$, not shown in Table 1), and those with covariates for recapture ranked relatively low (e.g. models 7–9; Table 2).

In contrast to birds from nonfumigated nests, survival of birds from fumigated nests increased linearly with nestling mass, and earlier hatching dates were favoured (Table 3b). There was a positive effect of colony size on survival in two years (Table 3b). There was little effect of

brood size on first-year survival (Fig. 3, Table 3b). Estimated survival in relation to nestling mass in fumigated nests showed nestlings of greater mass consistently having higher survival (Fig. 4). Peak survival was at the extreme upper limit of the nestling-mass categories, generally 7–8 g higher than the modal mass category for birds from fumigated nests in most years. Results for other years were similar to those shown in Figs 3 and 4.

Table 2 Representative mark–recapture models to explore first-year survival (*S*) and recapture (*p*) in cliff swallows for birds from fumigated nests[†].

Model #	S:brood	S:brood ²	S:mass	S:mass ²	S:*size	S:fleas	S:date	S:*date	S:*brood	S:*brood ²	S:*mass	S:*mass ²	<i>p</i> :mass	<i>p</i> :mass ²	<i>p</i> .*	<i>p</i> .*	<i>p</i> .*	$\Delta QAIC_c$	$\Delta QAIC_c$	# parameters
1	X				X	X	X											14 181.383	0	56
2		X			X	X		X										14 183.618	2.235	67
3	X		X		X	X	X											14 183.748	2.365	56
4	X		X		X	X	X											14 183.819	2.436	57
5	X		X		X	X	X	X										14 184.071	2.688	62
6	X		X		X	X	X	X										14 185.643	4.260	58
7		X			X	X	X	X			X							14 185.829	4.446	69
8	X		X		X	X	X	X			X	X						14 186.341	4.958	64
9			X		X	X	X	X	X		X	X						14 186.730	5.347	73
10			X		X	X	X	X	X		X	X						14 187.339	5.956	71
11			X		X	X	X	X	X	X			X					14 189.638	8.255	76
12			X		X	X	X	X	X	X	X							14 194.393	13.010	76
13	X		X		X	X	X	X										14 196.993	15.610	52
14			X		X	X	X	X	X						X			14 205.043	23.660	93
15					X	X	X	X	X						X			14 212.000	30.617	47

[†]Model parameterization for all was year- and age-dependent (first year, all others) for both survival (*S*) and recapture (*p*). Covariates included in each model are shown with an “X”. If denoted with *, covariates were year-specific. Covariate abbreviations: *brood*, brood size; *mass*, nestling mass; *size*, colony size; *fleas*, number of fleas per nestling; *date*, hatching date. Not all models tested are shown.

Table 3 Regression coefficients for effects on first-year survival in cliff swallows from nonfumigated and fumigated nests, with coefficients estimated from the top model (# 1) in Tables 1 and 2, respectively.

Variable	Regression coefficient (± 1 SE)
(a) Nonfumigated nests	
Brood size	0.164 (± 0.121)
(Brood size) ²	-0.114 (± 0.051)
Nestling mass	0.039 (± 0.136)
(Nestling mass) ²	-0.174 (± 0.083)
Bugs per nestling	-0.831 (± 0.329)
Fleas per nestling	0.204 (± 0.121)
Colony size (1982)	0.413 (0.200)
Colony size (1983)	0.653 (± 0.321)
Colony size (1984)	-1.982 (± 1.010)
Colony size (1986)	-0.975 (± 0.457)
Colony size (1987)	2.982 (± 1.865)
Colony size (1989)	-0.372 (± 2.163)
(b) Fumigated nests	
Brood size	-0.014 (± 0.055)
Nestling mass	0.043 (± 0.016)
Fleas per nestling	0.158 (± 0.115)
Hatching date	-0.013 (± 0.003)
Colony size (1984)	-0.0003 (± 0.0020)
Colony size (1985)	0.002 (± 0.0005)
Colony size (1986)	0.0007 (± 0.0003)
Colony size (1987)	0.0002 (± 0.0003)
Colony size (1988)	0.0002 (± 0.0002)
Colony size (1989)	-0.0003 (± 0.019)

Coefficients that were significant (95% CI not overlapping 0) are shown in boldface.

Discussion

In contrast to many studies of first-year survival in relation to nestling mass in birds (e.g. Kremenetz *et al.*, 1989; Lindén *et al.*, 1992; Monrós *et al.*, 2002; Garant *et al.*, 2004; Tinbergen & Sanz, 2004; Schwagmeyer & Mock, 2008; Braasch *et al.*, 2009; Cleasby *et al.*, 2010), we found evidence for relatively strong stabilizing selection on the intermediate (and also the most common) mass categories under natural conditions (i.e. in nonfumigated nests). And, in contrast to the few existing studies that detected birds of intermediate mass being favoured (Adriaensen *et al.*, 1998; Bouwhuis *et al.*, 2014), our comparison of patterns of survival in nonfumigated vs. fumigated nests seems to implicate parasitism by swallow bugs, not predation, as a potential driver of stabilizing selection on mass. We also found evidence for intermediate brood sizes being favoured. These effects occurred even while controlling for other potential effects, such as colony size and the number of bugs infesting a nest. To our knowledge, the only similar studies are on other swallow species, in which nestling survival to fledging seemed to peak at intermediate brood sizes when parasites were most numerous (Moss & Camin, 1970; Møller, 1991).

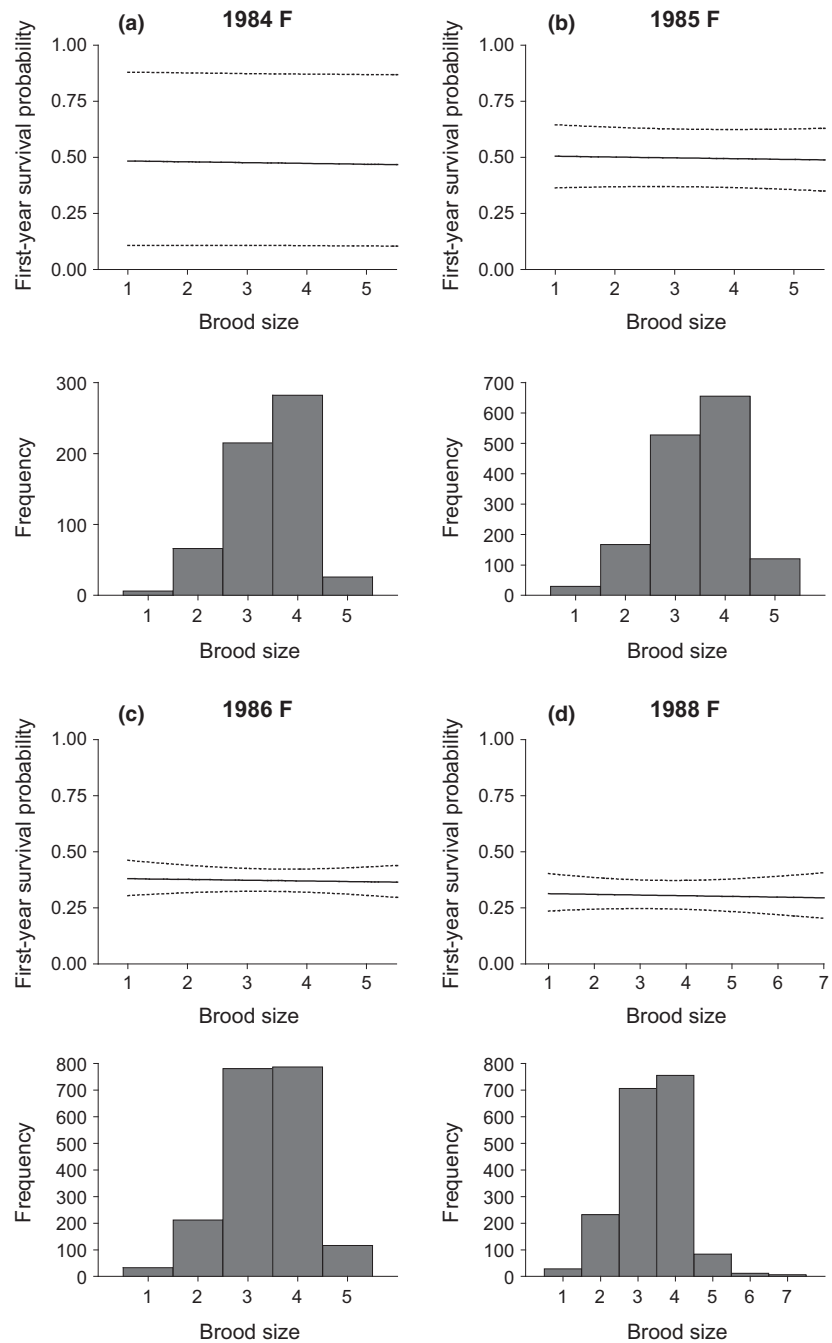


Fig. 3 Estimated first-year survival probabilities for cliff swallows from fumigated nests in relation to brood size, and the observed frequencies of brood sizes, in four representative years (a–d). Survival was estimated from the top model (model 1, Table 2), and curves shown were solved at mean values of all other covariates. Predicted survival is indicated with a solid line, and dotted lines show 95% confidence limits.

Effects on survival

The survival analysis identified a number of effects on first-year cliff swallow survival for birds in nonfumigated nests under natural conditions. Effects of colony size were similar to those documented earlier using a larger data set (Brown *et al.*, 2016), and the fact that colony size remained significant once accounting for the additional variables in this study strengthens the

earlier conclusion that survival selection based on colony size fluctuates in direction among years in the presence of parasites. Here, we also found the extent of parasitism by swallow bugs to be inversely related to first-year survival, an unsurprising result given the other deleterious effects of bugs on cliff swallows (Brown & Brown, 1986, 1996, 2004a).

The significant nonlinear (and nonsignificant linear) regression coefficients for both nestling mass and brood

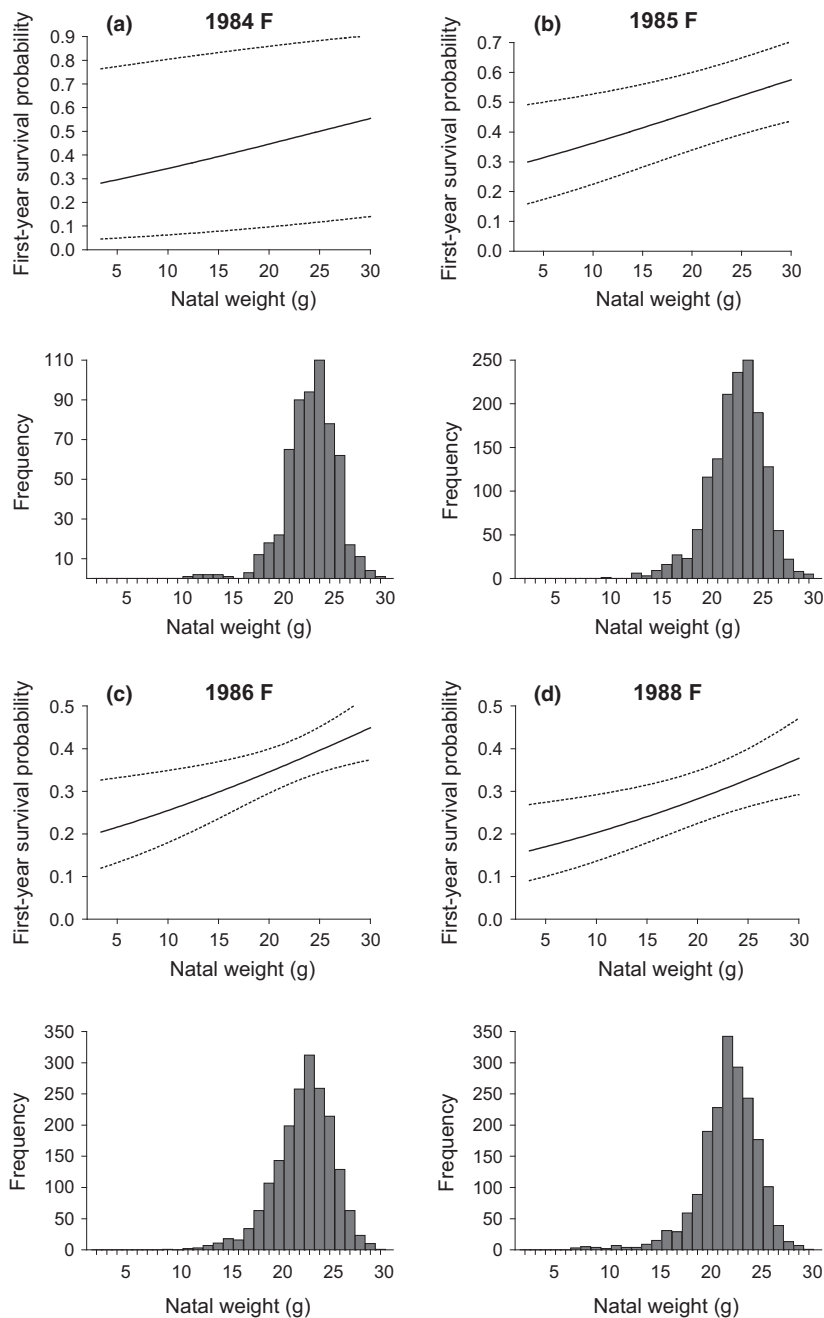


Fig. 4 Estimated first-year survival probabilities for cliff swallows from fumigated nests in relation to nestling mass (in g), and the observed frequencies of nestling mass categories, in four representative years (a–d). Survival was estimated from the top model (model 1, Table 2), and curves shown were solved at mean values of all other covariates. Predicted survival is indicated with a solid line, and dotted lines show 95% confidence limits.

size suggest possible stabilizing survival selection on these traits in the presence of parasites. Estimated survival was highest at the modal nestling mass and brood size, indicating an apparent intermediate optimum in each case that did not vary with year, at least over the 8-year period of our study.

In contrast, when bugs were removed by fumigation, evidence for stabilizing selection on nestling mass and brood size disappeared. Brood size had no effect, and nestling mass appeared to have a positive linear effect

on survival. Hatching date significantly affected first-year survival for birds from fumigated nests in most years, with earlier hatched nestlings surviving better. The results for fumigated nests are consistent with other analyses showing disadvantages of late nesting in the absence of parasites (Brown *et al.*, 2015). Interestingly, a date effect was not detected in nonfumigated nests, with hatching date not included in the top model. The other measured effects on nestlings in the presence of parasites likely swamped any date effect.

Effects of colony size for birds from fumigated nests, while significant in two years, were of relatively small magnitude. Because parasites have a role in driving fluctuating selection on colony size for first-year birds under natural conditions (Brown *et al.*, 2016), we would predict little effect of colony size in the absence of parasites, which is consistent with what we found in the present study.

Differences in natal dispersal could confound estimates of first-year survival and their associated covariates in mobile species such as cliff swallows. In great tits (*Parus major*), heavier birds were more likely to immigrate into a study area, whereas heavier birds were not more likely to emigrate, suggesting an interaction between habitat quality and dispersal (Verhulst *et al.*, 1997). Whether cliff swallow long-range dispersal depends on nestling mass or brood size is impossible to know, as few birds (< 10) were ever recovered outside the study area. However, at least within the study area, there was no difference in brood size or nestling mass among first-year birds returning to their natal colony site vs. to another site (Brown & Brown, 1992). This suggests no dispersal distance biases among the birds for which we estimated local apparent survival.

Effects of parasites

That cliff swallow nestlings of relatively low mass do not survive well is not surprising, and nestlings even in fumigated nests survived poorly if in the lower mass categories. This suggests that some of the disadvantages of low mass may be related to factors besides ectoparasites, such as low fat reserves that compromise young birds' ability to survive food stress soon after fledging while still dependent on their parents to find them and feed them (Naef-Daenzer *et al.*, 2001; Götmark, 2002; Medeiros & Freed, 2009; Gow & Wiebe, 2014). Parasites, however, may also contribute to low-mass nestlings being less likely to survive their first year, both through greater proportional blood loss (Brown & Brown, 2009) and by causing more asymmetric feather growth in poor-condition individuals during moult on the wintering grounds (Brown & Brown, 2002). Wing and tail asymmetry impairs foraging success in cliff swallows (Brown & Brown, 1998).

Parasites seem to manifest their effects primarily on higher-mass nestlings, where large birds were at a survival disadvantage. Predation seems likely not to be a cause for this pattern, unlike in other species (Adriansen *et al.*, 1998; Bouwhuis *et al.*, 2014); otherwise, we should have seen a similar survival cost at higher nestling masses in the absence of parasites, which we did not. One possible explanation is that swallow bugs prefer to feed on the largest nestlings in a brood, as has been documented for other ectoparasites in other systems (Roulin *et al.*, 2003; Valera *et al.*, 2004; Bize *et al.*, 2008). This might be because swallow bugs can feed

more safely and perhaps more quickly on heavier birds that are in good condition and not begging for food as much as their lighter nest mates. Feeding on a more quiescent host could be advantageous for bugs that (when engorged with blood) are susceptible to injury from host movement (C. and M. Brown, pers. obs.). Other blood-feeding insects feed more efficiently on bird hosts that are less active (Edman & Kale, 1971). More rapid, uninterrupted feeding and thus less time spent on the birds could mean bugs were less likely to be counted by us on the heavier nestlings, explaining in part why we detected an overall negative relationship between an individual's number of bugs and its mass.

More frequent feedings by bugs on heavier nestlings could be costly for those nestlings in the long term if these blood meals increase both total blood loss and the chance of transmission of potentially deleterious pathogens such as *Wolbachia* (Rasgon & Scott, 2004) and Buggy Creek virus (*Alphavirus*; O'Brien *et al.*, 2011). Swallow bugs are known to transmit both. In addition, the heavier (larger) nestlings also may present a greater target area, making them easier for bugs to locate, as reported for parasites on other taxa (Mohr, 1961; Zelman & Arai, 1998; Port & Boreham, 1980; Grutter & Poulin, 1998; Cable & van Oosterhout, 2007).

Brood size showed a similar pattern in which first-year survival under natural (nonfumigated) conditions peaked at an intermediate brood size each year. This pattern disappeared completely for fumigated nests, where there were no survival differences among brood sizes and again implicating a role of parasites for the nonfumigated nests. This result for nonfumigated nests could not be explained by a relationship between brood size and mass (with survival instead depending on mass), because nestling mass did not vary significantly with brood size, and our survival analysis included both variables. Thus, how could swallow bugs drive stabilizing selection on brood size?

It has been suggested that increases in brood size in birds can be a response to the presence of nest ectoparasites (Richner & Heeb, 1995). When such parasites have life cycles that are about the same length of time that nestlings are in the nest, a larger brood can dilute the per capita extent of parasitism and favour birds with larger broods (Dudaniec *et al.*, 2006; Norris *et al.*, 2010). Swallow bugs seem to be such parasites, as it takes an entire summer for bugs to produce a generation (Brown & Brown, 2005). We found that the number of bugs per nestling declined with brood size. This suggests that possibly higher rates of parasitism on the nestlings in the smaller broods could select against those individuals.

However, bugs must also be driving the drop in survival at the largest brood sizes, despite those nestlings having fewer observed bugs in general. In great tits and barn swallows (*Hirundo rustica*), nestlings in larger

broods had reduced measures of immune function (Hörak *et al.*, 1999; Saino *et al.*, 2002), perhaps as a result of nutritional stress. This could select against the largest broods if impaired immune function as nestlings extends into the first year. Whether this might apply to cliff swallows is unknown, but our results underscore the general point of Richner & Heeb (1995) that ectoparasites may affect brood-size evolution in birds.

Because we took into account variables such as hatching date, actual parasite load and colony size that are likely also to influence cliff swallow first-year survival, our analyses provide relatively strong evidence that parasites favour an intermediate number of offspring and an intermediate offspring size independently of other correlated variables. The fumigation helped establish that the patterns of survival differed only with respect to the presence of bugs. We tried to select nests and colonies for fumigation that differed as little as possible from the non-fumigated ones. However, we cannot discount that the absence of bugs may have led, for example, to changes in the behaviour of adult cliff swallows tending the fumigated nests. Parents may have adjusted their provisioning in unknown ways for nestlings that were less nutritionally stressed in the absence of bugs (Wesołowski, 2001; Bouslama *et al.*, 2002). Although counts of parental food deliveries and the quantity of insects delivered per trip (Brown & Brown, 1996) showed no obvious differences between birds occupying fumigated and nonfumigated nests (C. Brown, unpubl. data), there may still have been undetected parental responses to the lack of parasitism. These responses might have led in unknown ways to possibly artefactual results for the fumigated nests. Nevertheless, our results suggest a potentially novel (but still poorly understood) driver for stabilizing selection on nestling body mass and brood size, and join others in emphasizing the importance of parasites in life-history evolution in general (Gustafsson *et al.*, 1994; Martin *et al.*, 2001; Charmantier *et al.*, 2004b; Fitze *et al.*, 2004; Moreno *et al.*, 2005). Our analyses show that being heavier than average is not always best for small birds like cliff swallows, especially in the presence of parasites.

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