## Research

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# Can an introduced predator select for adaptive sex allocation?

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Most species produce equal numbers of sons and daughters, and sex differences in survival after parental care do not usually affect this pattern. Temporary overproduction of the scarcer sex can be adaptive when generations overlap, the sexes differ in life-history expectations, and parents can anticipate future mating opportunities. However, an alternative strategy of maximizing the competitiveness of the more abundant sex in these circumstances remains unexplored. We develop theory showing how mothers can maximize reproductive value when future mate competition will be high by producing more sons in the advantageous early hatching positions within their broods. Our model for optimal birth order was supported by long-term data of offspring sex in a parrot facing catastrophic female mortality caused by introduced predators. Swift parrots (*Lathamus discolor*) suffer high female mortality due to introduced sugar gliders (*Petaurus breviceps*) creating fluctuating male-biased adult sex ratios. Offspring hatched early within broods fledged in better condition, and in support of our model were more likely to be male in years with higher adult female mortality. We found a highly significant rank-order correlation between observed and predicted birth sex ratios. Our study shows the potential for mothers to maximize reproductive value via strategic biases in offspring sex depending on the advantages conferred by birth order and the predictability of future mate competition. Our long-term data support the predictions and appear to suggest that sex allocation strategies may evolve surprisingly quickly when anthropogenic pressures on populations are severe.

## 1. Introduction

In most taxa, sons and daughters are produced in equal numbers [1,2]. Sex allocation theory has successfully explained this pattern by asserting that an overproduction of one sex is balanced by a reduction in the average fitness for individuals of that sex [3,4]. Even cases where adult mortality is sex-biased should not normally lead to increased production of the rarer sex because the total reproductive output of males and females must always be equal. When an individual dies, the average reproductive output of the remaining individuals of that sex increases, leaving the benefit of producing sons or daughters unaffected [5,6].

It is important to realize that when sex-biased adult mortality fails to select for adjustment of offspring sex, the argument (in the simplest case) is based on random mating among the survivors. This means that the model assumes there are no traits that elevate the mating success of some males relative to others. Given this assumption, then even if achieving mating is harder for one sex than the other, there is no impact on reproductive values at the time when offspring are produced. If, say, few adult males succeed because female mortality exceeds male mortality (yielding an excess of males relative to females among

mature individuals), then the low prospects of daughters due to mortality and the low prospects of sons due to mating difficulties exactly cancel out [4].

Here, we point out that this cancelling out is no longer true if the prospects of sons depend on their birth order within a clutch, there are temporal dynamics where adult females are in particularly short supply in some years, and the strength of the relationship between male competitiveness and mating success varies accordingly. The logic is the following. Consider a population that has males of varying competitiveness, traceable back to their early life conditions. This setting may reward the more competitive males more strongly in certain years when achieving mating is particularly hard, while in years with a more favourable sex ratio (from the male perspective, i.e. many females), males may succeed relatively independently of their competitiveness. This argument requires that mating indeed becomes rather evenly distributed when the adult sex ratio is relatively balanced, which is likely for a pair-breeding species: female scarcity means that many males are bound to fail to secure a mate, while a sex ratio close to 1 : 1 means that most or even all males can succeed.

Our argument is similar to the Trivers–Willard hypothesis, where mothers capable of investing more in particular offspring should favour the production of the sex for which an increase in quality helps them in later mate competition [7–9]. However, our model replaces the causality that is based on the variable condition of mothers with two factors: within-clutch differences in birth order having an impact on condition [10,11] and the fact that the condition of males matters more, or less, depending on how many females have survived to be available as mates. This latter factor means that we also identify a new causal route to the finding that sex-specific mortality that differs predictably across cohorts, either cyclically or by perturbation, may allow mothers to make adaptive adjustments towards the offspring sex that will have more future mating opportunities [12,13]. Our model thus extends recent analyses that seek the specific circumstances under which sex-biased mortality after parental investment influences the birth sex ratio [14,15].

It is common in birds for earlier hatched offspring to have a head start in growth and development [16,17], and this 'silver spoon effect' [18] may confer advantages in later mate competition if the offspring are male. Mothers have been shown to use the silver spoon effect to promote the fitness of male offspring in size dimorphic species where the larger sex receives a greater advantage by hatching earlier [19–23] and in size monomorphic species with polygamous mating systems in which males benefit in terms of later mating success if hatched early in the sequence [11,24–27]. Hatching order may be less important for female offspring because it is typically easier for females to find a mate [4]. This is especially true in birds where adult sex ratios are usually male biased as a result of female-biased adult mortality [28], although it is important to note that the early life environment itself can also affect the lifetime reproductive and sex allocation strategies of females [29]. If this means intense male, but not female, competition for mates, the question arises as to whether a parent should bias offspring sex ratios such that early laid eggs are disproportionately male, and later eggs female?

Intuition suggests that the strength of selection on such a strategy depends on the predictability of the intensity of future sexual competition. Here we identify and analyse a system in which extraordinarily high, but spatially variable, adult female mortality leads to predictable variation of future mate competition. Critically endangered swift parrots (*Lathamus discolor*) suffer greater than 50% female mortality per year due to an introduced mammalian predator, the sugar glider (*Petaurus breviceps*), that accesses the nest hollows and kills females while they incubate eggs [30]. High predation on females is causing both severe population decline and strongly biased adult sex ratios (greater than or equal to 73% male) [31,32]. The birds are nomadic and gain a limited reprieve from sugar glider predation in years when ephemeral food resources allow them to nest on predator-free islands [33,34]. The highly variable rate of sugar glider predation on females (0–100% of nests) between years and sites [30], but not males together with an iteroparous life cycle, mean that males born in different years compete in the same mating pool later, while females born in different years contribute to the pool too, but less so when the year has been preceded by a poor survival year for females. Sugar gliders were introduced to swift parrot habitat relatively recently (mid nineteenth century [35]), which might suggest that females are unlikely to have evolved adaptive responses to this predator; nonetheless, the conditions *per se* (predictable variation in mating difficulties [12]) are suited to such responses evolving.

Here, we produce a simple reproductive value model (with no spatial movement between sites), as well as a spatial model variant tailored to the life history of these birds, to examine the fitness benefits of biasing early hatched offspring towards males in breeding seasons when predation on adult females is high. We then use the sex of over 500 nestlings over 7 years with highly variable rates of predation on breeding females to test the model predictions.

## 2. Material and methods

### (a) Study species

Swift parrots are migratory birds that breed along the eastern seaboard of the large island of Tasmania south of mainland Australia, as well as two smaller islands (Bruny and Maria) (figure 1) [36]. Swift parrots are nomadic within their breeding range to the extent that breeding may occur each year anywhere in eastern Tasmania where an appropriate combination of habitats (ephemerally flowering *Eucalyptus globulus* and *E. ovata*) and nesting habitat (tree cavities in the old-growth forest) occurs [33,34]. Population genetic studies confirmed that the population is panmictic with individuals likely to move between, and also spread out to use, different breeding locations within and between years [37]. Swift parrots are sexually monomorphic [38], lay a median clutch of four eggs (range = three to six eggs), and are socially, but not genetically, monogamous [31].

Sugar gliders are native to continental Australia, but were introduced to Tasmania in the nineteenth century [35,39,40]. They are now present at all swift parrot breeding sites thus far monitored on the main island of Tasmania, although rates of predation on breeding females vary considerably depending on forest cover (fragmented landscapes have higher predation due to sugar gliders) [30]. Sugar gliders are absent from Bruny and Maria Islands where the swift parrots sometimes breed [30] (figure 1). The data reported here were collected over seven breeding seasons (October–February) from 2010 to 2016 and included breeding sites where annual predation rates on breeding females ranged from 0% to 54%. We tested the predictions from our sex allocation models using the sexes of 501 nestlings over 161 broods.
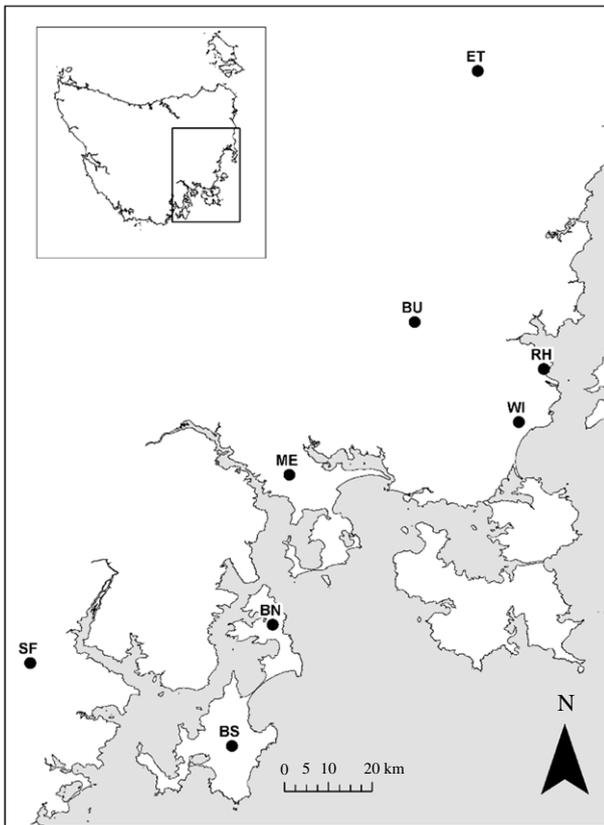
**Figure 1.** Map of the study area in Tasmania, Australia. Low predation sites included North Bruny Island (BN, no sugar glider predation on nesting females, $n = 38$ nests), South Bruny Island (BS, no sugar glider predation, $n = 20$ nests), Buckland (BU, predation rate $= 0.08$, $n = 19$), Meehan Range (ME, predation rate $= 0.14$, $n = 9$) and Wielangta (WI, predation rate $= 0.17$, $n = 7$). High predation sites included Southern Forests (SF, predation rate $= 0.50$, $n = 16$), Rheban (RH, predation rate $= 0.50$, $n = 6$) and Eastern Tiers (ET, predation rate $= 0.54$, $n = 29$).

## (b) Field and laboratory methods

Field and molecular methods are outlined in [30,31]. In brief, nest hollows in eight key breeding areas across eastern Tasmania were identified using behavioural cues of swift parrots and accessed using single rope climbing techniques. Nests were climbed while females were incubating eggs to ascertain clutch size. Nestling swift parrots were temporarily removed from their nests and blood was collected using brachial venepuncture and stored on FTA paper (Whatman) or in ethanol. DNA was extracted and used to genotype and molecularly sex all nestlings [31]. Data on both offspring sex and paternity (single versus multiple) were obtained for a subset of 273 nestlings from 91 broods [31].

We used the site-specific predation rates reported in [30,31]. In brief, we recorded the success or failure of all nest cavities visually using tree climbing and camera traps. Using the program MARK [41], we calculated daily nest-survival rates for eight regions, and converted these to the true nest-survival rate over the course of the 60-day nesting period. Sites and site-specific annual predation rates for breeding females (proportion killed) are provided in figure 1. This research was carried out under ANU Ethics protocol A2017/38 and under research license from the Tasmanian Government (Department Primary Industry, Parks, Water and Environment).

## (c) The models

### (i) The non-spatial model

Our non-spatial model investigates the reproductive value increase of early hatched (hatched first or second in sequence)

males relative to later-hatched males (hatched third or later), as adult female mortality increases. We compute the value for a scenario involving 10 000 nests, each with four eggs and 1 : 1 sex ratio across all eggs, thus we investigate reproductive values of 10 000 early hatched males competing against 10 000 later-hatched males. Note that this simple model does not yet assume any sex ratio biases, instead we simply examine how an assumed advantage of early hatched males translates (or fails to translate) into a higher reproductive value, depending on female availability. See the electronic supplementary material for the full development of the non-spatial model.

### (ii) The spatial model

The spatial model considers sex allocation with respect to hatch order tailored to the life history of *L. discolor*. Swift parrots breed once a year, producing an average brood of four eggs; in the model, we assumed the clutch size to be four. Birds breed on mainland Tasmania and in some years part of the population breeds on offshore islands; in the model, this translates to 50% of years being 'island years' during which 30% of the population was assumed to use islands while the remaining 70% remained as breeders on the mainland. In non-island years, all individuals bred on the mainland (these assumptions reflect observations over long-term field studies [33]). On mainland Tasmania, predation by the introduced sugar glider during nesting results in higher female mortality than male mortality. On offshore islands, there is no sex bias in mortality because sugar gliders are not present. In the models, we had four versions of this: we either included the female-biased mortality on islands or not, and we allowed sex allocation to depend on current location (mainland versus island) or not (see electronic supplementary material, table S1). The chosen annual mortality values (20%, 60%) reflect field data [30,32]. Across all four scenarios, the early hatched males had a mild (20%) competitive advantage over later-hatched males, but for this advantage to be realized there have to be fewer females in the population than males (otherwise all males mate even if some are less competitive). On average, therefore, we expect there to be little selection to adjust sex ratios in those scenarios where females never suffer higher mortality than males, but even here demographic stochasticity may cause (mild) mate shortages for either sex. See the electronic supplementary material for the full development of the spatial model. Models and simulations were constructed using MATLAB 2016b software [42].

## (d) Statistical analyses

We used linear mixed models to analyse the effect of hatch order on the body condition of 538 swift parrot nestlings over 7 years. Details of how body condition was measured, and model selection, are given in the electronic supplementary material.

Nestlings were assigned a binary response for sex (1 = male, 0 = female) and the variates associated with nestling sex were analysed using generalized linear mixed models with logit link function using package *lme4* v. 1.2.21 [43,44]. We tested for the effect of hatch rank (one-four, continuous variable), clutch size and the site-specific predation rate on nesting females. Time of season (i.e. Day) was tested and controlled for in all analyses by including as a covariate the number of days since the first breeding attempt by any bird within the same season. Nest hollows were not usually reused within or between seasons and were only used once in each analysis here. Adults were banded (ringed) opportunistically and the number of banded birds was a small proportion (less than 10%) of the population each year. No banded individuals were studied repeatedly between seasons. Study site and year were included as random terms in all models. A saturated model was first fitted, including all two-way interactions excluding the study site. Non-significant interaction terms were then removed from the model, which was then dredged using *MuMIn* v.1.43.17

[43,45] to identify the five most parsimonious models based on the lowest Akaike information criteria values with correction for small sample size (AICc).

Nestling survival was similarly assigned a binary response (1 = survived to fledging) and analysed as above with the addition of offspring sex as a fixed effect. All statistical analyses were conducted in R [46].

## 3. Results

### (a) Model predictions

Our non-spatial reproductive value model predicts that it is possible for mothers to maximize the reproductive value of their brood by biasing the sex of early hatched young towards males if the mortality of adult females is high (figure 2a). The same model indicates that the increase in reproductive value via this mechanism ceases to occur if female and male lifespans are equal (note that we assume no difference in maturation rate, which potentially maintained such differences in an earlier study on kestrels [11]). Our spatial model, tailored explicitly to the highly variable site-specific mortality experienced by wild swift parrots, mirrored these predictions by tracking a single population's evolution when the choice of breeding locations varies over the years, leading to different primary sex ratios produced in different years. When the model did not differentiate between island and mainland sites the sex ratio of early hatched offspring in the simulations eventually became male biased. This happened more quickly when predation on females was higher than for males (figure 2b,d). However, when females bred at both island (low predation) and mainland (high predation) sites the sex ratio of early hatched nestlings was predicted to become more male biased at the island sites but not on the mainland (figure 2c,e). The male bias in early hatched offspring evolved more quickly in the model when predation on breeding females was higher than that for males (figure 2c).

### (b) Nestling condition

Our data supported the major premise of the above models that early hatched nestlings are likely to have higher reproductive value because they receive an advantage in terms of fledging in better body condition. The best model of body condition index (BCI) included an effect of ordinal hatch order and an effect of year of birth. The models tested and their AICc scores are shown in electronic supplementary material, tables S2 and S3. The effect of hatch order is shown in figure 3.

### (c) Nestling sex

The overall brood sex ratio (proportion males) of 0.52 did not differ significantly from parity (one-tailed binomial test, $p = 0.17$). However, our results provide strong support for the key model prediction that females in high predation sites should bias the sex ratio of early hatched nestlings within broods towards males (figure 2c). The best model included the terms Hatch rank, predation level, Time of season (Day), Year of study, and the interactions Hatch rank * predation level and Day * Year of study. The Hatch rank * predation level interaction was included in each of the top five models ($\Delta$AICc = 0.68, Wi = 0.32, electronic supplementary material, tables S4 and S5), and raw data showing this effect are plotted in figure 4a. Importantly,

and in keeping with the prediction above, figure 4a shows that females at low predation sites on islands and the mainland did not show biases in the sex ratio for early hatched offspring. A highly significant rank-order correlation confirmed that differences in the birth sex ratio between early (those hatched first and second) and late hatched (third or later) nestlings increased as predation on adult females increased ($t = 7.61$, $p < 0.001$, bootstrapped $r = 0.962 \pm 0.03$ s.e., 1000 samples, figure 4b).

Our data did not support alternative hypotheses that might account for male bias among early hatched nestlings. Although included in the top models selected by AICc (electronic supplementary material, tables S4 and S5) the time within breeding season ('day' after the first clutch initiated) was not significant ($p = 0.99$). The interaction between day and hatch rank was not included in the best model (electronic supplementary material, table S5). Similarly, there was no evidence that mothers favour either sex in any hatch position (first to last) to maximize nestling survival (electronic supplementary material, table S6). There was no evidence that nestlings were more likely to be male if they were progeny at nests with extra-pair mating for any particular hatch rank ($p = 0.235$).

## 4. Discussion

The severe predation on breeding female swift parrots [32] presents an unusual opportunity to study the impacts of perturbations in the adult sex ratio on sex allocation strategies. In principle, it is already known that mothers can optimize fitness by manipulating offspring sex based on the differential benefits of birth order [10,11,25,27]. Our study investigated this effect in a system where adult sex ratios vary depending on the choice of breeding location and the consequent mortality risk for females, leading to subsequent variation in the intensity of competition between males. Our long-term field data supported the predictions of our models by showing that male offspring were favoured early in the hatching sequence in breeding seasons when adult mortality was especially high for females (figure 4). The models demonstrated proof-of-principle, but did not specify the timescale required for such traits to evolve, and support for their predictions was correlational. Nonetheless, the fit of the data to the predictions appeared to be robust, with the tendency towards males in early hatched positions occurring less in low predation sites regardless of whether they were on mainland Tasmania or offshore islands.

Our models make two key assumptions. The first one is the 'silver spoon' effect of hatching first [18], which we assume to increase a nestling male's body condition and later competitiveness. There is a wide-spread trend to this effect across species [16,17,47] and it is supported in swift parrots by our long-term data showing that nestlings hatched early in the sequence fledged with better body condition (figure 3).

The second key assumption is that, despite the recency (mid-nineteenth century [35]) of the invasive predator causing female mortality to exceed greatly male mortality (depending on the breeding site chosen by the population each year), females have evolved to adjust the sex ratio of early eggs in the appropriate direction. The genetic mechanisms underpinning sex allocation are still poorly understood [48,49], and our more complex and best-supported model (figure 2c) assumes that a breeding female can modify offspring sex
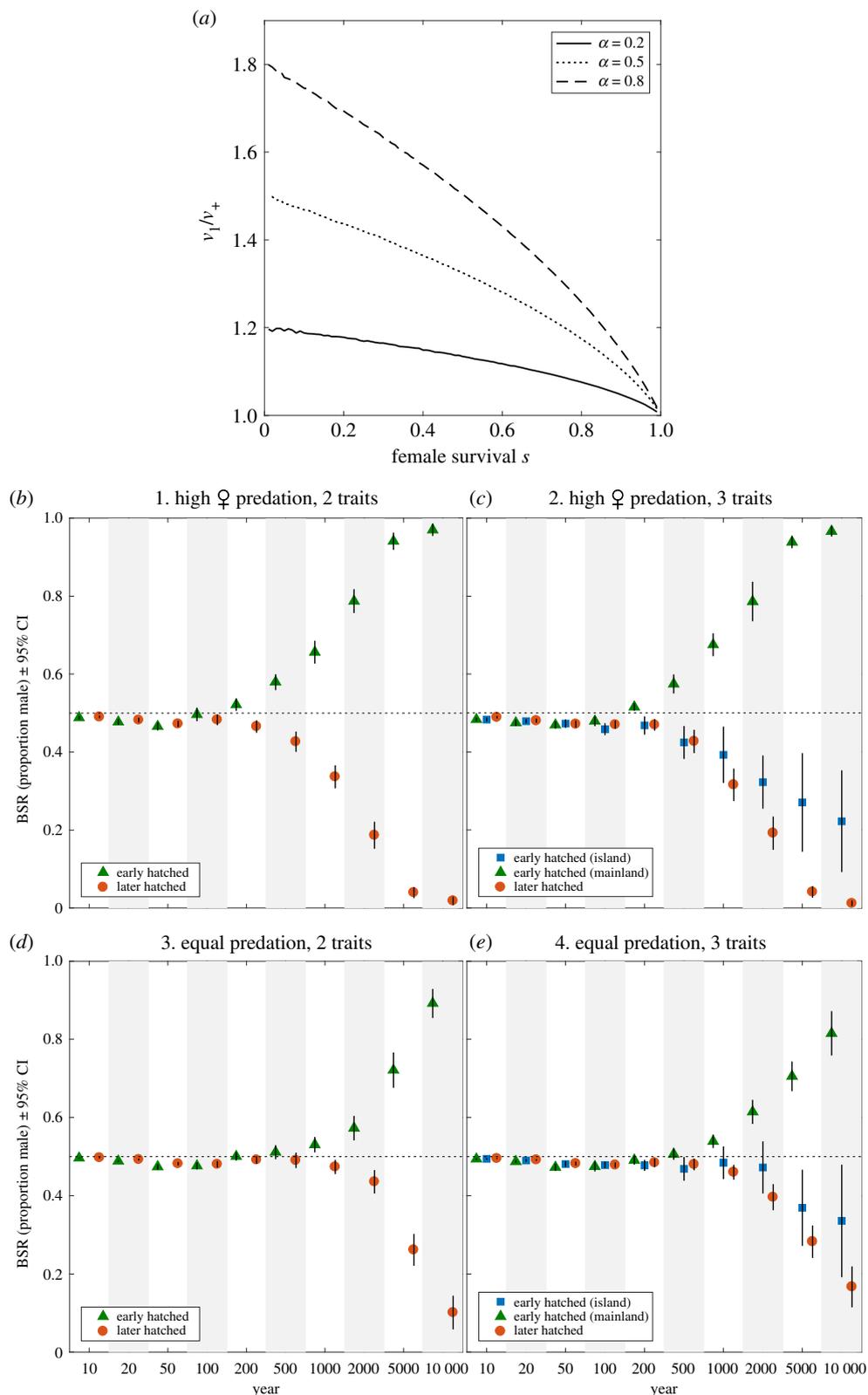
**Figure 2.** Predictions from reproductive value model and spatial model tailored to the life history of swift parrots. (a) Ratio of reproductive values of early hatched to later-hatched males ($V_1/V_+$) against increasing female survival s (expressed as a proportion of male survival). Output for three values of $\alpha$ (relative competitiveness, 0.2, 0.5, 0.8) is shown. Values are shown where s ranges from 0 to 0.99 in steps of 0.01. (b−e) Predictions from four modelled scenarios over 10 000 years of the birth sex ratio of early versus late hatched nestlings (±s.e.). Scenarios 1 and 2 (b,c) reflect the higher mortality on adult females than males when the birds breed at mainland Tasmanian sites. Scenarios 2 and 4 (c,e) allow offspring sex ratios on islands (low female mortality) and at mainland Tasmanian sites (high female mortality) to evolve independently (three traits instead of two). Scenario 2 (c), where females can evolve to allocate sex of offspring differentially depending on whether they breed at high or low predation sites, provides the key prediction that females at high predation sites will bias the BSR of early hatched offspring towards males. (Online version in colour.)

depending on information about the extent of future mating competition derived from current breeding circumstances. The field data suggest mothers are capable of doing this,

since the extent of sex bias was found to depend on breeding in risky versus non-risky areas. The panmictic nature of the species and the likelihood that the birds cannot predict
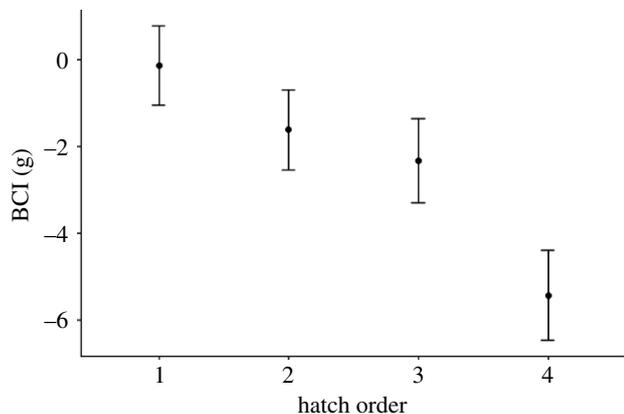
**Figure 3.** Mean body condition index (BCI) ± s.e. against hatch order of eggs in swift parrot clutches.



**Figure 4.** Birth sex ratios, showing the effects of hatch rank and predation rate on adult females. (*a*) Birth sex ratio (BSR, or proportion sons) against nestling hatch rank at sites on offshore islands (two sites with no predation on adult females by sugar gliders), mainland sites with low sugar glider predation (three sites with less than 17% female mortality/year) and mainland sites with high sugar glider predation (three sites with greater than 50% female mortality/year). (*b*) Difference in BSR (proportion males) between early hatched (first + second) and late hatched (third or later) nestlings against the annual predation rate of nesting adult females at eight ephemeral breeding locations in Tasmania. Data are from 501 nestlings (161 broods) breeding at eight sites over 7 years.

where they will breed in subsequent years also suggests that females adjust sex allocation in response to the impact of female mortality in one season on the whole population in subsequent years.

This raises the question of the mechanism, should the pattern prove robust: what is the cue that provides the breeding females with critical information concerning the extent of local predation [4]? Given that swift parrots are not very long lived (maximum lifespan 8.8 years [50]), and individuals breed at just one site per year, and that there are multiple areas to choose from, it is unlikely that individual-level learning of predation risk can take place—especially since the most dramatic learning event (an actual attack on an incubating female) typically does not lead to the now 'informed' female surviving. One alternative is that they use the extent of current male–male competition, particularly the number of unpaired males seeking copulations [31] as a guide to the extent of likely future mate competition. Male–male competition has been shown to be more intense with higher rates of polyandry observed at the sites where predation on females is highest [28]. Another plausible proximate mechanism is that females alter their sex ratios in response to higher stress in high predation sites, especially if they are aware of higher predator density or subject to more attacks. Glucocorticoids are known to influence offspring sex ratios in various birds species [51] and could account for the apparently fast evolutionary change in swift parrot sex allocation (see below) but it is unclear how such a mechanism would produce a bias only in early hatched offspring.

Finally, there is the question of how rapidly a sex ratio bias can evolve. Due to the lack of information regarding genetic architecture, the cues used by females, or any ancestral (prior to the invasion of the predator) sex ratio patterns, we cannot offer a test that would investigate the match between model predictions and data regarding the timeline for adaptive sex allocation to evolve. We, therefore, consider our models and data to be a proof-of-principle study, demonstrating the plausibility of the argument that flexible sex allocation has evolved since the advent of extreme sex-biased mortality in swift parrots in historical times (e.g. between 100 and 250 years, figure 2*c*). The predator responsible for heightened mortality of breeding females was introduced to Tasmania in the mid-nineteenth century and probably took several decades to spread throughout the state and impact widely on swift parrots [35,39,40], leaving at least a century for selection to lead to the patterns of sex allocation observed in this study.
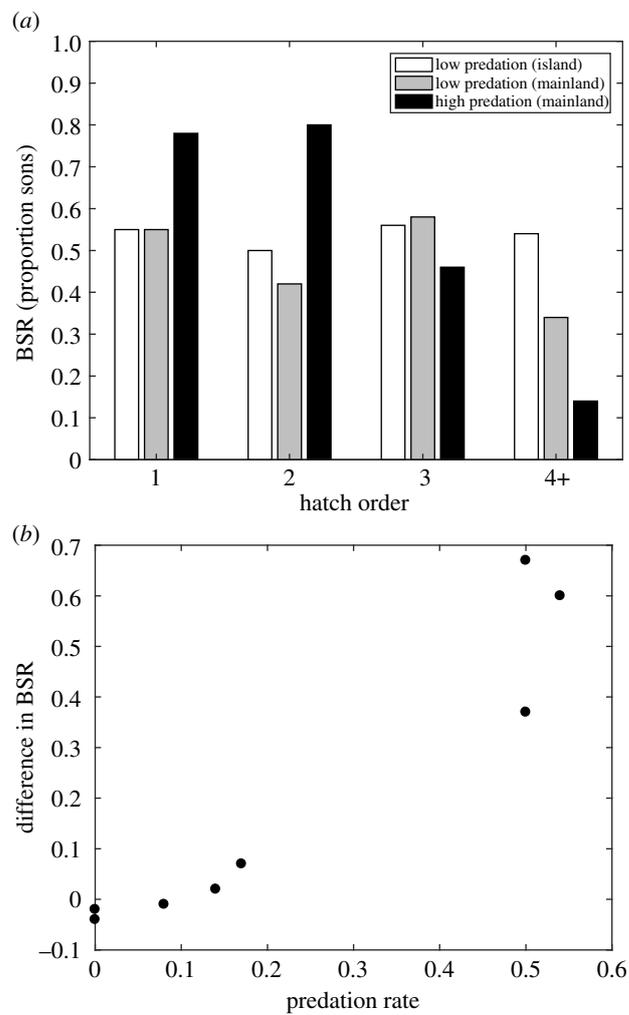
In any case, the study confirms that there is no response to heightened female mortality that would take the form of overproduction of females, regardless of the desirability of such a response from the angle of conservation. Sex ratio theory has proven efficacy for the practical management of some threatened populations [52,53], but in this case, does not lead to any obvious options for slowing the dramatic decline identified for swift parrots [28,29].

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