Year: 2014

The hawk–dove game in a sexually reproducing species explains a colourful polymorphism of an endangered bird

Kokko, Hanna ; Griffith, Simon C ; Pryke, Sarah R

Royal Society Publishing

The hawk–dove game in a sexually reproducing species explains a colourful polymorphism of an endangered bird

Hanna Kokko[1,2], Simon C. Griffith[3] and Sarah R. Pryke[1,3]

[1]Centre of Excellence in Biological Interactions, Division of Ecology, Evolution and Genetics, Research School of Biology, Australian National University, Canberra, Australian Capital Territory 0200, Australia
[2]Wissenschaftskolleg zu Berlin, Institute for Advanced Study, Wallotstrasse 19, 14193 Berlin, Germany
[3]Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia

The hawk–dove game famously introduced strategic game theory thinking into biology and forms the basis of arguments for limited aggression in animal populations. However, aggressive 'hawks' and peaceful 'doves', with strategies inherited in a discrete manner, have never been documented in a real animal population. Thus, the applicability of game-theoretic arguments to real populations might be contested. Here, we show that the head-colour polymorphism of red and black Gouldian finches (*Erythrura gouldiae*) provides a real-life example. The aggressive red morph is behaviourally dominant and successfully invades black populations, but when red 'hawks' become too common, their fitness is severely compromised (via decreased parental ability). We also investigate the effects of real-life deviations, particularly sexual reproduction, from the simple original game, which assumed asexual reproduction. A protected polymorphism requires mate choice to be sufficiently assortative. Assortative mating is adaptive for individuals because of genetic incompatibilities affecting hybrid offspring fitness, but by allowing red 'hawks' to persist, it also leads to significantly reduced population sizes. Because reductions in male contributions to parental care are generally known to lead to lower population productivity in birds, we expect zero-sum competition to often have wide ranging population consequences.

1. Introduction

The introduction of the hawk–dove game into evolutionary thinking provided the cornerstone for our understanding of frequency-dependent contexts of animal behaviour [1]. This theoretical work not only showed that aggression can remain adaptively limited in animal populations, but also laid the basis for understanding behavioural polymorphisms in general. Despite one real-life example of a plastic response to current mating status [2], there is a remarkable lack of any empirical illustrations of the game being played out in nature by discrete morphs, with genetic inheritance of the relevant strategies.

The Gouldian finch is an endangered and declining bird that occurs in northern Australia. It exhibits three colour morphs in both males and females, one of which (yellow) occurs very infrequently (approx. one in 2000 birds [3]) and plays an insignificant role in population dynamics. Here, we model the population dynamics of the Gouldian finch, taking advantage of the established genetic and behavioural differences between the two main head-colour morphs—red and black. The head-colour allele occurs on the Z chromosome and impacts behaviour and the hormonal profiles of birds: red individuals are behaviourally dominant [4,5] and have significantly higher levels of testosterone and corticosterone in response to socially competitive environments [4], which makes us equate them with the 'hawk' type—the type that gains easy access to critical resources—in the hawk–dove game. The species is an obligate cavity nester: cavities offer protection from nest predators, and their availability and variation in their quality can severely constrain reproduction [5], which forms the basis of higher reproductive success of hawks among individuals

that are predominantly 'doves'. Because of the ZZ–ZW sex determination system of birds, hawks (red individuals) can be genetically *RR* or *Rr* if male (homogametic sex), or *R* if female (heterogametic sex). Doves (black individuals) are *rr* if male, and *r* if female [6]. Clutch sizes and the survival of sons and daughters are known for each combination of inter-breeding morph genotypes [7,8], with clear signs of genetic incompatibilities in offspring leading to reduced reproductive success in broods where the parents form a mixed pair (red paired with black). Unsurprisingly, therefore, mating is assor-tative with respect to colour [4].

Our aim is to show that the polymorphism in the finch system can be understood using the hawk–dove framework, while real-life biological detail (stemming from sexual repro-duction) adds to the dynamics that the game predicts. The two defining features of the hawk–dove game are that hawks, when rare, (i) gain access to resources easily, but (ii) suffer negative fitness consequences when interacting with each other in populations where hawks have become common [1]. Red 'hawk' Gouldian finches (i) have priority access to suitable tree cavities that are essential for breeding [9,10]; in our model, we denote this with $k > 1$. Simul-taneously, (ii) the breeding success of nesting pairs where the male is red declines with an increasing proportion of reds in the local population [11]. The reduced success in rearing young is associated with increased aggression (testosterone) and stress (corticosterone), compromised health [4] and a reduction in paternal care by red adults in red-dominated populations [11]. We show below that this has negative popu-lation-level consequences, but this does not remove the red morph from the population as the priority access to cavities favours the red morph when it is rare.

2. The model

(a) Overview

The Gouldian finch is an endangered species with the current total population probably only just exceeding 2500 [12]. For this reason, it is both feasible and necessary to include sto-chastic variation in local population sizes (which can be small) and morph ratios. We do this by opting for an individ-ual-based model, where we use published data (see the electronic supplementary material) to consider reproduction of individuals located across n habitat patches and b breeding sites per patch. The model tracks the fate of each individual on an annual basis until it dies. Note that the original hawk–dove game assumed asexual reproduction for simpli-city [1]. As birds reproduce sexually, and the strategies are determined by loci on sex chromosomes, there is the potential for far richer dynamics than the original game predicted, especially because it is known that Gouldian finches bias off-spring sex ratios in response to the phenotype of the breeding pair [13]. Each individual is therefore characterized by geno-type, sex, nest site (whether it has a good quality tree hollow) and the nature of the parental pair (i.e. the combination of parental genotypes; hereafter called 'origin').

Following known morph determination rules [6], a bird's genotype can take values *R* or *r* for females, and *RR*, *Rr* or *rr* for males. The state variable origin therefore takes six differ-ent values depending on the genotypes of the parents of the bird, although some combinations are not possible. Thus, for example, a mother that is *r* cannot produce an *RR* male. The
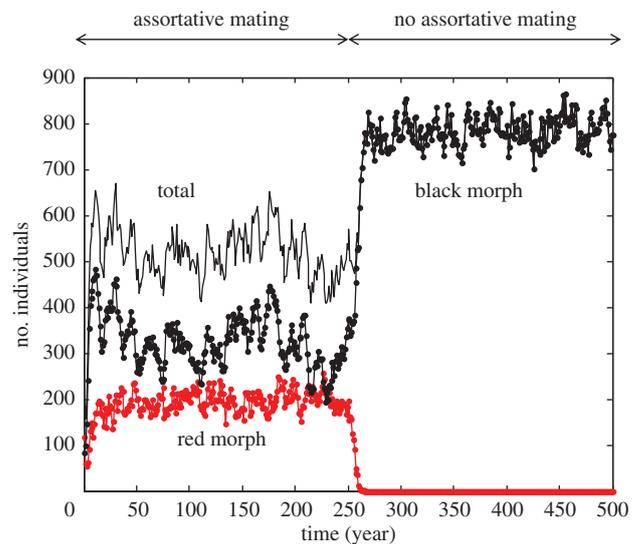

Figure 1. A time series of a population with parameters $s = 0.7$, $f = 1$, $k = 2$, $n = b = 10$, and the population initiated with 100 females and 100 males, with each colour allele being red with probability 0.5. Assortative mating is assumed to occur with strength $a = 5$ until generation 250, after which it is assumed to be absent ($a = 1$). The polymorphism is maintained until the red morph goes extinct in the absence of assortative mating. In the absence of the red morph, the population reaches a much higher equilibrium size than before.

model therefore takes into account that the number of off-spring of each genotype produced by a breeding pair depends on parental genotypes, and the population-wide output consequently also depends on likelihood of different types of pairings (see the electronic supplementary material). These likelihoods depend on the strength of assortative mating preferences, which have an adaptive basis due to gen-etic incompatibilities between red 'hawks' and black 'doves' [7,8]. The strength of assortative mating is denoted a. Here, $a = 1$ denotes random mating (neither hawk nor dove females express a preference for own morph over the other). Populations with $a > 1$ mate assortatively with respect to head colour: hawks prefer to mate with hawks, doves with doves, the preference becoming stronger with a.

The model also needs to incorporate the fact that hawks (pairs in which the male is *RR* or *Rr*) have a competitive advantage in contests over nest sites, but the breeding success of such pairs declines with increasing hawk density. We assume the competitive advantage is characterized by a parameter $k > 1$, reflecting elevated success of hawks (by a factor k) when a good nest site is contested. The fre-quency-dependent decline in breeding success, in turn, is characterized using parameter f. Here, $f = 1$ corresponds to data (see the electronic supplementary material), $f > 1$ makes the decline steeper than in real data, and $f = 0$ removes the frequency-dependent effect entirely.

To derive the distribution of morphs in each year, we used known relationships between parental phenotypes, clutch size, sex ratio and sex- and morph-specific survival of offspring (see the electronic supplementary material). As annual survival is probably lower in the wild than in aviary conditions, we modi-fied aviary based sex- and morph-specific survival values by multiplying them with a parameter s ($0 < s \leq 1$).

The model always stabilizes quickly (figure 1), leading to either a clear protected polymorphism or extinction of one or both morphs within 500 years. To achieve a visual impression

3

rspb.royalsocietypublishing.org Proc. R. Soc. B 281: 20141794

of changes that are causally related to a particular parameter simultaneously with the impact of stochastic variability, we present our results as 'mosaics' where the colour at each parameter combination indicates the population size or composition at generation 500 of a single run of the simulation.

(b) Details of the simulation

One run of the model begins with an initialization stage, when we assume that the frequency of the red allele is x. The initial population consists of F_0 females and M_0 males, with each of their colour alleles (one for females and two for males) randomly chosen as R (probability x) or r (probability $1-x$). Initially, no individual has a nest, and their origin variables take randomly chosen values among all logically possible maternal and paternal genotype values. Strictly speaking, randomly chosen values do not perfectly capture situations where some matings are more likely than others for current values of assortative mating. This unavoidable problem persists for one generation only, as the populations in generation 2 are already formed by tracking the correct distribution of matings.

After initialization, each year of the population is computed as follows.

(1) Each individual is assigned randomly to one of n habitat patches. Each patch i is assumed to have b breeding sites (nest hollows) available. The number of individuals of a given sex that attempt to breed in site i may exceed the number of breeding sites at site i.

(2) Females within each location are randomized in terms of the order in which they can choose mates. The probability of the female choosing a particular male is proportional to his attractiveness, determined through assortative preferences: a male's attractiveness for a particular female is 1 if his morph differs from that of the female, and a if it matches that of the female ($a \geq 1$). Chosen males become unavailable as social mates for subsequently choosing females, reflecting the real constraints of a socially monogamous mating system. Males who reside in a different habitat patch are also unavailable. Thus, if $a = 5$, and a focal hawk (red) female has two hawk (red) males and one dove (black) male to choose from, the probability of her choosing the first hawk is the same as her choosing the second hawk (both are $5/(5 + 5 + 1) = 0.455$), while the dove male is chosen with probability $1/(5 + 5 + 1) = 0.09$. Note that if the local sex ratio differs from $1:1$, some individuals of the surplus sex remain without a mate.

(3) The social pairs compete for nest sites. Individuals who remained single do not take part in this competition, and birds cannot see nest sites outside their local habitat patch. Pairs with a hawk male have a competitive advantage of magnitude $k \geq 1$. The probability that a particular pair gains access to a particular nest is calculated similarly to above. A nest effectively 'chooses a pair to own it' proportionally to the pair's competitiveness, which equals 1 for pairs with a dove male and k for pairs with a hawk male. Nests gain owners in this way until there are no vacant nests available or there are no pairs left.

(4) Each nest-possessing pair breeds. The clutch size is determined probabilistically, with distributions extracted from field data (electronic supplementary material, table S1). The probability that an egg is male follows electronic supplementary material, table S2. The egg-to-recruit

probabilities, i.e. survival from egg to a yearling, depend on the genotypes of the father, the mother and the chick, as well as on the local proportion of hawks (electronic supplementary material, table S3).

(5) In addition to recruits, some adult individuals also survive to the next year. Survival consists of two components: relative and absolute. Relative survival is derived from known relationships between own and parental genotypes as indicated in the electronic supplementary material, table S4. These values are based on aviary studies; thus we use the multiplier s to indicate survival in the wild, which presumably falls below that in the aviary (thus $0 < s \leq 1$).

(6) After recruitment and adult survival have been computed, the time count is updated from year t to year $t + 1$. Reflecting the dispersive habits of the Gouldian finch, all individuals are assumed to redistribute themselves again in the following year (thus no bird keeps its nest or its mate).

Steps 1–6 were repeated for 500 years, which in all cases proved to be sufficient to have a population stabilize at a protected polymorphism or—in cases where survival s is low—to lead to extinction (electronic supplementary material, figure S1).

The main results are therefore derived by computing a large number of runs, each with a subtly different parameter value combination. Our preference for producing mosaics with a large number of adjacent subtly different parameter values, rather than a large number of replicates with a single parameter value combination, is based on arguments [14,15] that this forms the most efficient use of computer time: it allows one to simultaneously estimate the shape of any relationship (e.g. the parameter region in which the total population is likely to go extinct), as well as the relevant variability. For example, if only 30% of populations go extinct in a particular parameter region, this is visible as a case where slight shifts in parameter values do not produce a sharp boundary between extinction and persistence but a mosaic pattern with roughly 30% of parameter choices leading to extinction.

3. Results

The degree of assortative mating proves pivotal for the continued persistence of both morphs (figure 1). When assortative mating was removed in the model (by setting $a = 1$), polymorphism was never maintained (see example in figure 1), regardless of other parameter values (10 000 trials with freely chosen f-values, followed by another 10 000 with the data-driven value of $f = 1$). Without frequency-dependent breeding success of hawks ($f = 0$), polymorphism was likewise never maintained (10 000 trials). Thus, both a decline in hawk reproductive success with hawk frequency (the original feature of the hawk–dove game) and assortative mating (a consequence of sexual reproduction) are required for the polymorphism to be protected. Successful breeding requires investment in contests over nest sites (a zero-sum competitive situation where one individual's win is another's loss), as well as parenting expenditure. Since improvements in parenting ability benefit populations more than increased investment in any competitive trait associated with zero-sum competition, we expect investment in nest-site competition at the expense of parenting to have negative population consequences. The negative population effect is strongly visible in the model, as Gouldian
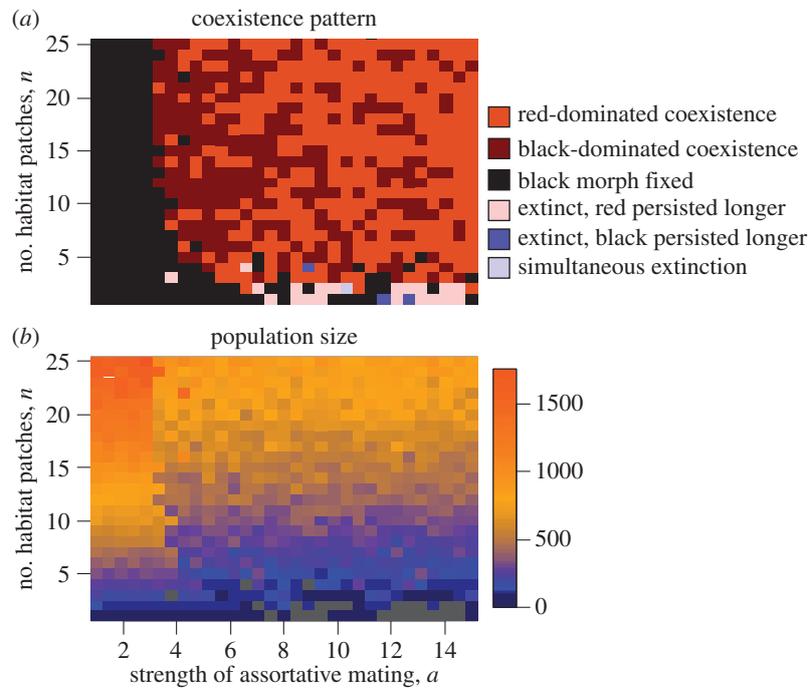
Figure 2. Population state after 500 generations for different numbers of habitat patches, n, and strength of assortative mating, a, when $f = 1$, $k = 3$, $s = 0.65$ and $b = 10$. (*a*) The colour of each square depicts the classification of the population state: hawk-only (bright red), dove-only (black), coexistence with a majority of hawks (light reddish colour), coexistence with a majority of doves (dark reddish colour), extinction with hawks persisting for longer (purple), extinction with doves persisting for longer (dark blue), and extinction with both morphs having persisted for equally many generations before extinction (light blue). (*b*) The total number of individuals at generation 500.

finches are predicted to need much more habitat to reach a given population size when coexisting as a polymorphism, than in cases where blacks (the morph that invests less in zero-sum components of fitness) are the only surviving morph (figure 2*a,b*). This match between the patterns of coexistence and the ensuing population size is repeated across varying values of other parameters, such as survival, local carrying capacity of habitat patches and the relative hawk advantage at different hawk–dove frequencies (electronic supplementary material, figures S1 and S2).

Both severe habitat destruction and low survival are predicted to lead to extinction, preceded by the disappearance of red hawks (electronic supplementary material, figures S1 and S2). This suggests that monitoring changes in the proportion of different colour morphs can be useful in conservation programmes. Counterintuitively, severe declines in population size, including extinction, can occur in areas of particularly unfortunate combinations of parameter values that set the rules for morph coexistence. For example, both morphs can go extinct when annual survival is relatively high, whereas one of them (black) persists indefinitely when survival of adults is lower ('valley of death', pink region in the electronic supplementary material, figure S1). This is a case of evolutionary suicide *sensu* [16]: extinction does not occur because of intrinsic problems of habitat availability or survival, but because morph frequencies evolve in an unsustainable direction. In this population fitness valley, hawks are competent enough to take over nest sites from doves and to breed relatively successfully, but are still not successful enough to maintain the productivity of the population in the absence of the healthy population growth that doves provide. Hawk-only persistence is also possible, but only in the theoretical case where they perform much better at parenting than indicated by current empirical data (electronic supplementary material, figure S1).

4. Discussion

Our results show that the simplifying assumptions of the hawk–dove game are replaced by more complex dynamics in a real-life setting. The Gouldian finch, with a polymorphism of behaviours that differ dramatically in their relationship to population fitness, can show very surprising and diverse population-level responses to challenges such as reduced survival or habitat deterioration. There is clear scope for investigating further issues such as the behavioural decisions of individuals that fail to secure a nest site: we assumed that they cannot disperse to a new site before the current breeding season is over, but this constraint may be less severe in reality. However, it is unclear whether behaviourally subordinate individuals would easily find better options elsewhere, given that the species forms mixed-colour populations throughout its range [3]—thus black individuals cannot easily avoid encountering the superior nest-site competitor by dispersing. This situation has been exacerbated by the reduction in the supply of suitable tree cavities across the range of the species, through changes over the past century in landscape processes such as fire which have reduced the number of mature trees bearing suitably sized hollows [17].

Morph frequencies can have a significant impact on population dynamics [18,19]. Indeed, recent reviews state an expectation that polymorphisms should be beneficial for population persistence and growth [20]. The morphs of the Gouldian finch, however, yield insight into the possibility that selection favours behaviours detrimental for population fitness and species persistence [21–24]. Individual fitness is often subject to trade-offs between components that have a direct, positive relationship with population fitness (e.g. parental care) and those that instead reflect success in zero-sum games (e.g. competition over paternity, nest ownership). In

5

rspb.royalsocietypublishing.org   Proc. R. Soc. B 281: 20141794

zero-sum games, one individual's win is another's loss, and better performance (hawk-like behaviour) does not elevate population fitness [25,26]. Therefore, whenever success in zero-sum games forms a part of individual fitness, selection may favour underinvestment in traits that population growth relies on [21]. This is a particularly strong expectation in sexually reproducing species because male life histories often feature competition of a zero-sum nature over paternity [27].

We also found that the polymorphism was not maintained in the absence of assortative mating. This finding is interesting, as at first sight it appears to contrast with existing literature where it is suggested that assortative mating (which is adaptive if there is gene flow between incipient species and hybrid fitness is compromised) could lead to reduced gene flow and ultimately speciation, i.e. a clearly different outcome to a within-species colour polymorphism [28,29]. The two species may then fail to coexist, in which case assortative mating would ultimately lead to the persistence of only one colour morph [28]—while we found this outcome (monomorphism) precisely when there was no assortative mating.

To explain the apparent discrepancy, it is important to note that published arguments we refer to [28,29] consider processes on time scales far longer than those assumed in our model: we did not model selection on assortative mating, and the consequent evolutionary changes in this variable. Instead, our model complements the field by highlighting the possibility of a faster process operating over ecological time scales: one of the morphs may completely fail to persist if mating is random or only weakly assortative. This happens because of *positive* frequency dependence [30]: whichever morph is initially common (black under most of our parameter settings), its individuals enjoy elevated reproductive success under random mating because they usually pair with a mate of their own colour, thus avoiding genetic incompatibility issues. Put another way, the rare morph suffers a cost of being rare due to incompatibility with the majority of available mates and is lost from the population. This outcome is avoided (i.e. the polymorphism is maintained) if a sufficiently large fraction of individuals of the rare morph can avoid mating with incompatible mates, which they can if mating is sufficiently assortative.

Although this system is possibly unique in its details, which include the morph-specific quality of male care, male contributions to parental care can have very general consequences for population productivity. In a dataset of 980 bird species, it was recently found that female-only care leads to an approximately 20% reduction of population productivity [31], which suggests that our results generalize widely. It is also of interest to note that populations riddled with internal conflict can become weaker interspecific competitors [32,33]. In the Gouldian finch, nest-site competition is intensified by the presence of heterospecific finch competitors [34]. If the presence of heterospecific competitors favours hawk-like behaviours, within-population investment may shift even further away from good parenting, and indeed a recent study confirmed that hawk-like red Gouldians were more competitive against a heterospecific nest-site competitor [5].

Discrete polymorphisms of a striking visual and genetically discrete nature are relatively rare, which has no doubt hampered the search for real-life examples of the theoretically predicted classic models of animal conflict [1]. Although the Gouldian finch system has certain features that make the case unusually clear (e.g. the genetic basis of the polymorphic trait is known), the endangered nature of this species also presents challenges with respect to model validation aims. Specifically, given that conservation goals take priority, it is not possible to translocate individuals at varying morph ratios to found new populations, to track the subsequent dynamics in the field. However, there is no reason why the relevant hormonal and behavioural categories could not remain present, but perhaps in a less easily detectable form, in a number of species, in which they are not as clearly signalled through an associated colour polymorphism.

References

1. Maynard Smith J, Price GR. 1973 The logic of animal conflict. *Nature* **246**, 15–18. (doi:10.1038/246015a0)

2. Fromhage L, Schneider JM. 2005 Virgin doves and mated hawks: contest behaviour in a spider. *Anim. Behav.* **70**, 1099–1104. (doi:10.1016/j.anbehav. 2005.02.020)

3. Gilby A, Pryke SR, Griffith SC. 2009 The historical frequency of head-colour morphs in the Gouldian finch (*Erythrura gouldiae*). *Emu* **109**, 222–229. (doi:10.1071/MU09013)

4. Pryke SR, Astheimer LB, Buttemer WA, Griffith SC. 2007 Frequency-dependent physiological trade-offs between competing colour morphs. *Biol. Lett.* **3**, 494–497. (doi:10.1098/rsbl.2007.0213)

5. Brazill-Boast J, Griffith SC, Pryke SR. 2013 Morph-dependent resource acquisition and fitness in a polymorphic bird. *Evol. Ecol.* **27**, 1189–1198. (doi:10.1007/s10682-013-9651-1)

6. Southern HN. 1945 Polymorphism in *Poephila gouldiae*. *J. Genet.* **47**, 51–57. (doi:10.1007/BF02989037)

7. Pryke SR, Griffith SC. 2009 Postzygotic genetic incompatibility between sympatric color morphs. *Evolution* **63**, 793–798. (doi:10.1111/j.1558-5646. 2008.00584.x)

8. Pryke SR. 2010 Sex chromosome linkage of mate preference and color signal maintains assortative mating between interbreeding finch morphs. *Evolution* **64**, 1301–1310. (doi:10.1111/j.1558-5646.2009.00897.x)

9. Pryke SR, Griffith SC. 2006 Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. *Proc. R. Soc. B* **273**, 949–957. (doi:10.1098/rspb.2005.3362)

10. Pryke SR. 2007 Fiery red heads: female dominance among head color morphs in the Gouldian finch. *Behav. Ecol.* **18**, 621–627. (doi:10.1093/beheco/arm020)

11. Pryke SR, Griffith SC. 2009 Socially mediated trade-offs between aggression and parental effort in competing color morphs. *Am. Nat.* **174**, 455–464. (doi:10.1086/605376)

12. Garnett S, Szabo J, Dutson G. 2010 *The action plan for Australian birds 2010*. Collingwood, Victoria: CSIRO Publishing.

13. Pryke SR, Griffith SC. 2009 Genetic incompatibility drives sex allocation and maternal investment in a

polymorphic finch. *Science* **323**, 1605–1607. (doi:10.1126/science.1168928)

14. Cottingham KL, Lennon JT, Brown BL. 2005 Knowing when to draw the line: designing more informative ecological experiments. *Front. Ecol. Environ.* **3**, 145–152. (doi:10.1890/1540-9295(2005)003[0145:KWTDTL]2.0.CO;2)

15. Kokko H, Jennions MD. 2010 Behavioral ecology: the natural history of evolutionary biology. In *Evolution since Darwin: the first 150 years* (eds MA Bell, WF Eanes, DF Futuyma), pp. 291–318. Sunderland, MA: Sinauer.

16. Dieckmann U, Metz JAJ. 2006 Surprising evolutionary predictions from enhanced ecological realism. *Theor. Popul. Biol.* **69**, 263–281. (doi:10.1016/j.tpb.2005.12.001)

17. Brazill-Boast J, Dessmann JK, Davies GTO, Pryke SR, Griffith SC. 2011 Breeding habitat selection in the endangered Gouldian finch (*Erythrura gouldiae*) at two spatial scales. *Emu* **111**, 304–311. (doi:10.1071/MU10064)

18. Sinervo B, Lively CM. 1996 The rock–paper–scissors game and the evolution of alternative male strategies. *Nature* **380**, 240–243. (doi:10.1038/380240a0)

19. Sinervo B, Svensson E, Comendant T. 2000 Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* **406**, 985–988. (doi:10.1038/35023149)

20. Wennersten L, Forsman A. 2012 Population-level consequences of polymorphism, plasticity and randomized phenotype switching: a review of predictions. *Biol. Rev.* **87**, 756–767. (doi:10.1111/j.1469-185X.2012.00231.x)

21. Rankin DJ, Bargum K, Kokko H. 2007 The tragedy of the commons in evolutionary biology. *Trends Ecol. Evol.* **22**, 643–651. (doi:10.1016/j.tree.2007.07.009)

22. Rankin DJ, Dieckmann U, Kokko H. 2011 Sexual conflict and the tragedy of the commons. *Am. Nat.* **177**, 780–791. (doi:10.1086/659947)

23. López-Sepulcre A, Norris K, Kokko H. 2009 Reproductive conflict delays the recovery of an endangered social species. *J. Anim. Ecol.* **78**, 219–225. (doi:10.1111/j.1365-2656.2008.01475.x)

24. Connallon T, Cox RM, Calsbeek R. 2010 Fitness consequences of sex-specific selection. *Evolution* **64**, 1671–1682. (doi:10.1111/j.1558-5646.2009.00934.x)

25. Le Galliard JF, Fitze PS, Ferrière R, Clobert J. 2005 Sex ratio bias, male aggression, and population collapse in lizards. *Proc. Natl Acad. Sci. USA* **102**, 18 231–18 236. (doi:10.1073/pnas.0505172102)

26. Eldakar OT, Dlugos MJ, Pepper JW, Wilson DS. 2009 Population structure mediates sexual conflict in water striders. *Science* **326**, 816. (doi:10.1126/science.1180183)

27. Lehtonen J, Jennions MD, Kokko H. 2012 The many costs of sex. *Trends Ecol. Evol.* **27**, 172–178. (doi:10.1016/j.tree.2011.09.016)

28. Roulin A. 2004 The evolution, maintenance and adaptive function of genetic colour polymorphism in birds. *Biol. Rev.* **79**, 815–848. (doi:10.1017/S1464793104006487)

29. Gray SM, McKinnon JS. 2007 Linking color polymorphism maintenance and speciation. *Trends Ecol. Evol.* **22**, 71–79. (doi:10.1016/j.tree.2006.10.005)

30. Lehtonen J, Kokko H. 2012 Positive feedback and alternative stable states in inbreeding, cooperation, sex roles and other evolutionary processes. *Phil. Trans. R. Soc. B* **367**, 211–221. (doi:10.1098/rstb.2011.0177)

31. Sibly RM, Witt CC, Wright NA, Venditti C, Jetz W, Brown JH. 2012 Energetics, lifestyle, and reproduction in birds. *Proc. Natl Acad. Sci. USA* **109**, 10 937–10 941. (doi:10.1073/pnas.1206512109)

32. Rankin DJ, López-Sepulcre A, Foster KR, Kokko H. 2007 Species-level selection reduces selfishness through competitive exclusion. *J. Evol. Biol.* **20**, 1459–1468. (doi:10.1111/j.1420-9101.2007.01337.x)

33. Korb J, Foster KR. 2010 Ecological competition favours cooperation in termite societies. *Ecol. Lett.* **13**, 754–760. (doi:10.1111/j.1461-0248.2010.01471.x)

34. Brazill-Boast J, van Rooij E, Pryke SR, Griffith SC. 2011 Interference from long-tailed finches constrains reproduction in the endangered Gouldian finch. *J. Anim. Ecol* **80**, 39–48. (doi:10.1111/j.1365-2656.2010.01756.x)