Social Role Specialization Promotes Cooperation between Parents

Zoltán Barta,[1,*] **Tamás Székely,**[2,3] **András Liker,**[4] **and Freya Harrison**[2,5,†]

1. MTA-DE (Hungarian Academy of Sciences–University of Debrecen) "Lendület" Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, Egyetem tér 1, 4032 Debrecen, Hungary; 2. Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, United Kingdom; 3. Department of Animal Behaviour, University of Bielefeld, P.O. Box 10 01 31, 33501 Bielefeld, Germany; and Department for Sociobiology/Anthropology, Johann-Friedrich-Blumenbach Institute for Zoology and Anthropology, University of Göttingen, Kellnerweg 6, D-37077 Göttingen, Germany; 4. Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom; and Department of Limnology, University of Pannonia, 8200 Veszprém, Hungary; 5. School of Life Sciences, Centre for Biomolecular Science, University of Nottingham, Nottingham NG7 2RD, United Kingdom

abstract: Biparental care of offspring is a widespread social behavior, and various ecological, life-history, and demographic factors have been proposed to explain its evolution and maintenance. Raising offspring generally requires several types of care (e.g., feeding, brooding, and defense), and males and females often specialize in providing different types of care. However, theoretical models of care often assume that care is a single variable and hence that a unit of care by the mother is interchangeable with a unit of care by the father. We hypothesize that the ability of one parent to provide all types of care may be limited by nonadditive costs or by sex-based asymmetries in the costs of particular care types. Using an individual-based simulation, we show that synergistic costs of investing in two tasks or negligible sex-based cost asymmetries select for task specialization and biparental care. Biparental care persists despite intense sexual selection and sex-biased mortality, suggesting that previous models make overly restrictive predictions of the conditions under which cooperation can be maintained. Our model provides a mechanistic underpinning for published models that show that the synergistic benefits of individuals cooperating can stabilize cooperation, both in the context of parental care and in other social scenarios.

Keywords: evolutionary simulation, mortality, parental care, sexual selection, social evolution.

Introduction

By providing care to its young, a parent can earn direct fitness benefits in the form of increased survival and/or

reproduction of their offspring. However, care is also costly because caring parents can be taken by predators and/or the energy cost of rearing young may precipitate into lower postcare survival or future reproduction. Parents, therefore, face a trade-off between their own current and future reproductive success (Hamilton 1964; Owens and Bennett 1994). Biparental care—which occurs in various insects, fishes, frogs, birds, and mammals (Clutton-Brock 1991; Tallamy 2001; Reynolds et al. 2002; Cockburn 2006; Royle et al. 2012)—is a form of cooperation because the offspring represent a joint public good: each parent's costly investment provides benefits to itself and to its mate. This creates conflict between parents: because they are usually not related to one another, each stands to gain by deserting the current brood and shifting the full cost of care onto its mate (Trivers 1972; Lessells 1999; Houston et al. 2005).

A rich theoretical literature has explored the ecological, demographic, and behavioral factors that influence how this dilemma is resolved and has identified when natural and sexual selection should favor uniparental versus biparental care. Fundamentally, biparental care will be maintained if one parent cannot successfully raise offspring alone (Maynard Smith 1977; Houston et al. 2013) or if biparental care can increase offspring fitness more than the fitness gained by the deserting parent via remating or increased survival (Grafen and Sibly 1978; Yamamura and Tsuji 1993). Early models of the fitness payoffs of different reproductive strategies have inspired more complex explorations of how the evolution of parental care systems is influenced by variables such as adult sex ratio (McNamara et al. 2000; Kokko and Jennions 2008), sexual selection (Kokko and Jennions 2008; Alonzo 2012), energetic reserves (Barta et al. 2002), and behavioral rules parents follow in responding to one another's care deci-

sions (McNamara et al. 1999, 2003; Johnstone and Hinde 2006). Key predictions of these models have been extensively tested in various species and ecological settings (Harrison et al. 2009; Trillmich 2010; reviewed by Alonzo 2010; McGraw et al. 2010; Lessells 2012).

One aspect of parental care, however, has not received detailed attention from evolutionary theorists—the proposition that specialization by males and females into different care tasks may favor biparental care (Grafen and Sibly 1978; Motro 1994; Kokko and Jennions 2008; Lessells 2012). Specialization may lead to synergistic (more than additive) fitness benefits of biparental care accruing to offspring—in extreme cases, making a lone parent unable to raise any offspring—and may also constrain how each parent can respond to changes in its mate's care behavior (see Harrison et al. 2009). Young animals typically require various types of care: parents may incubate or brood their offspring, feed and nurture them, and protect them from predators and conspecifics. The extent to which males and females perform (non)overlapping sets of these behaviors shows conspicuous interspecific variation, and some species show clear sex-specific task specialization. As an example, in figure 1, we summarize the frequency of parental task specialization in birds. Sex-based task specialization is also commonly observed in biparental insect species, with marked role division in bark beetles, dung beetles, burying beetles, and ambrosia beetles (reviewed by Trumbo 2012). Task specialization may occur on a gross scale (e.g., in raptors, females typically incubate the eggs and chicks, while males hunt for food for their mate and their offspring) or may be very fine grained (e.g., in the dung beetle *Canthon cyanellus*, both parents move the first dung ball to the nest burrow, the male pushing and the female pulling, the male excavates under the ball, and then the female covers it with soil; Trumbo 2012). Despite the fact that sex-based specialization in different components of offspring care is known in many biparental species and despite verbal discussions of how task specialization may favor biparental care (e.g., Kokko and Jennions 2008; Lessells 2012), previous theoretical analyses of parental behavior have largely ignored that care is fundamentally a multidimensional trait (Royle et al. 2012; Székely et al. 2013) and simply modeled care as a univariate quantity, assuming that one unit of care by the female is equal to (and interchangeable with) one unit of care by the male.

A notable exception is the work of Grafen and Sibly (1978), who showed mathematically that if sex-based care specialization exists, it can promote the maintenance of biparental care. However, this study does not explain how care specialization evolves in the first place, which is important given that specialization is meaningless under uniparental care. An exploration of how task specialization and biparental care might coevolve is still conspicuous by its absence from the literature. Here we present the first parental care model that investigates the origin of sex-based care specialization and the concomitant stabilization of biparental care. We explore two mechanisms by which care specialization can arise: (i) greater-than-additive costs of investing in two distinct parental care roles (e.g., feeding versus defending the young) and (ii) a slight sex-based asymmetry in the costs of these two tasks.

We use an evolutionary simulation where two types of parental activity (care) are required to successfully raise offspring and introduce either (i) a synergistic cost of contemporaneously investing in different types of care or (ii) sex-based asymmetry in the costs of investing in care types. These scenarios are easily envisaged: some types of care cannot be performed simultaneously (e.g., incubating eggs, foraging for food, and defending the nest from predators are mutually exclusive), and in some cases one behavior increases the cost of a second behavior (e.g., in birds, leaving a clutch to forage imposes an additional cost of rewarming the eggs on returning; Deeming 2002). Sexually dimorphic traits may also lead to asymmetric costs of care (e.g., in species with sexual size dimorphism, incubation and brooding will be energetically cheaper for the larger sex; Székely et al. 2007).

By systematically manipulating the degree of cost synergism or sex-based asymmetry in costs, we investigate whether any of these scenarios leads to the emergence of sex-based specialization in a single type of care and, in turn, more equal sharing of labor between males and females in a population otherwise characterized by uniparental care. We also test whether role specialization makes cooperation more robust to intense sexual selection and sex-biased mortality, since the latter processes usually destabilize parental cooperation (Kokko and Jennions 2008). Our evolutionary simulation is based on a full population model with density-dependent feedbacks where mating rates are self-consistently derived, satisfying the Fisher condition that each offspring has two genetic parents (Kokko and Jennions 2008). An important consequence of the Fisher condition is that the rarer sex has a mating advantage compared with the more common one. Kokko and Jennions (2008) have shown that the negative frequency dependency generated by this condition has important effects on the evolution of parental care: any deviation from biparental care in a population where the adult sex ratio is 1 : 1 and the sexes are the same apart from the level of initial investment in parental care would start a self-correcting process, which results in a return to equal levels of care. This happens because the sex that cares less becomes commoner in the mating pool, which, by the Fisher condition, decreases its mating success, leading to increased benefits of caring.
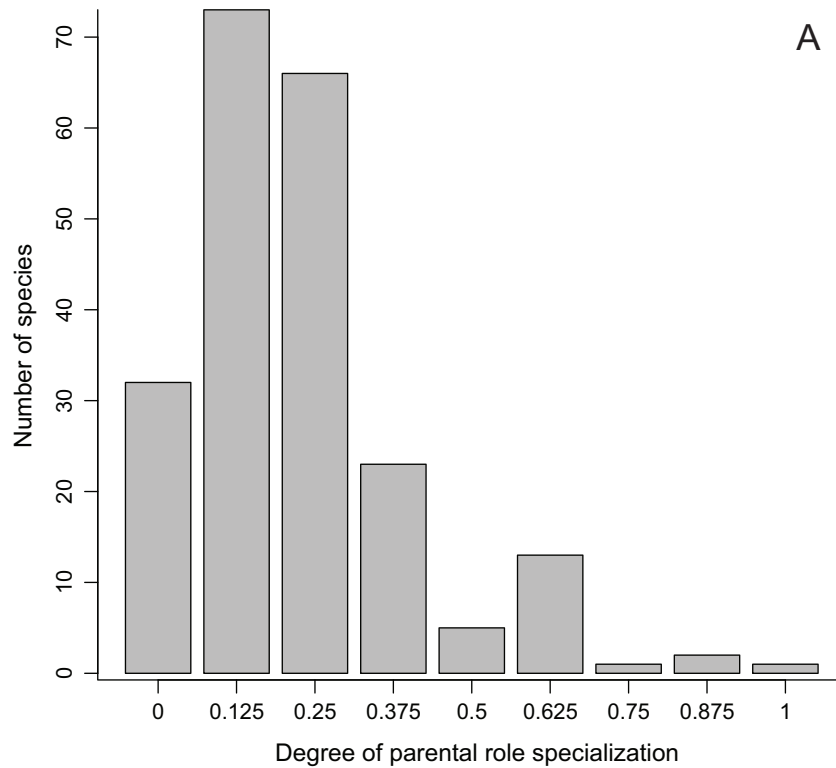
Figure 1: *A,* Incidence of social role specialization in birds. The proportional contributions of males to four care behaviors (nest building, incubation, chick brooding, and chick feeding) were quantified for 216 bird species (see the appendix, available online). For each species, we calculated the variance in male contribution across the four behaviors (scaled between 0 and 1) as a proxy for parental role specialization. Zero means no specialization (i.e., entirely overlapping male and female tasks), whereas values >0.5 reflect strong role specialization: females take the main (or exclusive) responsibility for one care behavior and males for a second care behavior. *B,* Male (foreground) and female African fish eagles (*Haliaeetus vocifer*; photo by T. Székely). Raptors are among the most parental care role-specialized birds. The female incubates and guards the chicks, while the male provides the majority of food for the chicks.

Analysis

Model

To investigate how task specialization affects the evolution of parental care, we developed an individual-based evolutionary simulation using the "time in, time out" framework (fig. 2). This framework is widely employed to study sexual selection and parental care (e.g., Grafen and Sibly 1978; Clutton-Brock and Parker 1992; Kokko and Jennions 2008). In this approach, individuals can be either single and hence available to mate (i.e., spending their time in the mating pool) or engaged and hence unable to mate because they are providing care (i.e., spending time out of the mating pool; Kokko and Jennions 2008). Time is discretized in our model, and the transition of individuals from one state to the other happens once in a time unit. Individuals switch from state in to state out as the result of mating, where mating probability depends on the frequency of both sexes, their encounter rate, and the strength of sexual selection (see below). Parents, that is, individuals in state out, provide care by allocating effort into two distinct care tasks, for instance, feeding the young and defending them from predators. Parents return to state in from state out after finishing care. The allocation of effort and the length of care are governed by the individual's genes. Individuals can die in any time unit, but their probability of mortality can depend on their sex and state. Our model parameters and their baseline values are provided in table 1; a detailed description of the model now follows.

In each time unit, single individuals of both sexes seek partners with which to mate. This is modeled as choosing one male and one female randomly from the pools of singles for $\min(N_m, N_f) \times r_{mating}$ times. Here, N_m and N_f are the number of single males and number of single females, respectively, while r_{mating} ($r_{mating} \leq 1$) describes how often individuals encounter one another. This formulation allows for fulfillment of the Fisher condition; that is, each individual has exactly one mother and one father (Kokko and Jennions 2008). Consequently, members of the minority sex have an advantage in acquiring a mate compared with those of the other sex (see above). We also consider sexual selection: nonrandom variance in mating success (Andersson 1994). Under sexual selection, some individuals with specific attributes are consistently more successful in acquiring a mate than others of the same sex lacking the given attributes. As a consequence, individuals that have mated have higher than average success in mating again. This increases the benefits of leaving the offspring; therefore, sexual selection can strongly favor desertion by the sex in which variance in mating success is nonrandom (Clutton-Brock 1991; Kokko and Jennions 2008; Alonzo 2010, 2012). To introduce sexual selection into the model, we allow the mating probability of individuals that have mated previously to be higher than that of those individuals that have never mated before (Kokko and Jennions 2008). To achieve this effect, the probability that the two chosen individuals form a mated pair and produce offspring is given by $m_m \times m_f$. If an individual has mated before, then $m_s = 1$ ($s = m, f$). On the other hand, $m_s = 1/k_s$, $k_s \geq 1$ ($s = m, f$) if a male or a female has never mated. Consequently, the mating probability of a never-mated individual can be less than 1. In this way, a mated individual's status predicts its future mating success; that is, we introduced a nonrandom variance in mat-
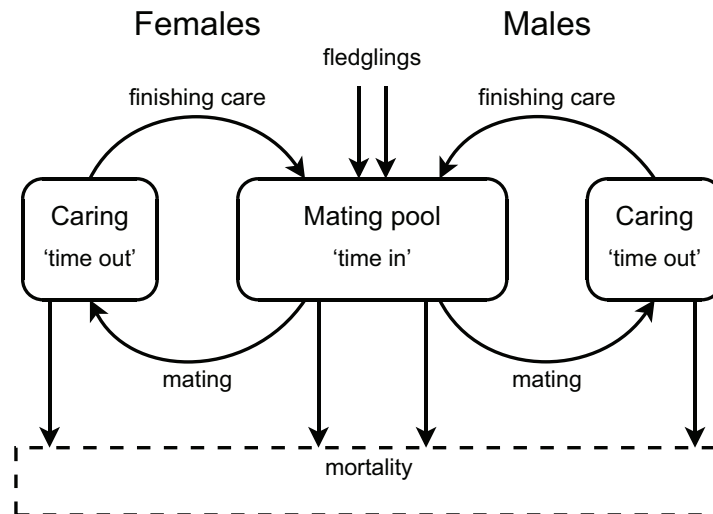

Females   Males

fledglings

finishing care   finishing care

| Caring 'time out' | Mating pool 'time in' | Caring 'time out' |

mating   mating

mortality

Figure 2: Schematic of the "time in, time out" model.

Table 1: Parameters of the model and their baseline values

Description	Symbol	Value
Cost of performing task i alone, $i = 1, 2$	C_i	1
Synergistic cost of performing both tasks simultaneously	C_3	0
Benefit of receiving type i care alone, $i = 1, 2$	B_i	1
Synergistic benefit of receiving both types of care simultaneously	B_3	0
Skill difference	Δ	0
Measure of variance in mating success for males and females, respectively	k_m, k_f	1, 1
Encounter rate for mate-searching individuals	r_{mating}	.1
Length of care by males and females, respectively	L_m, L_f	0–25, 0–25
Proportion of effort invested into task 1	A_m, A_f	0–1, 0–1
Parameter controlling the shape of survival curve	α	.2
Clutch size	n_{young}	1
Background mortality	M_b	.1
Strength of density dependence	δ	1.5
Carrying capacity	K	5,000
Mortality of single males and females, respectively	$M_{S,m}$, $M_{S,f}$	.2, .2
Parameter affecting the mortality of caring males and females, respectively	$\mu_{C,m}$, $\mu_{C,f}$	.2, .2
Mutation rate		.001
SD of deviance occurring during mutation		.05

ing success (Kokko and Jennions 2008). We consider the parameter k_s to be a measure of strength of sexual selection on sex s (Kokko and Jennions 2008).

An individual's behavior is governed by its genes. Each individual has two homologous chromosomes (i.e., they are diploids). Each chromosome contains four alleles with sex-limited expression (hence, each chromosome carries four loci, two of which are not expressed in a given individual). In males, alleles L_m govern length of care (i.e., the time out; Kokko and Jennions 2008) and alleles A_m govern how much effort a caring male allocates to the two care tasks. Likewise, a female's behavior is determined by L_f (length of care) and A_f (allocation of care). The actual values of L_s and A_s are the averages of the corresponding allelic values, and allelic values fall between 0 and 1. The value of L_s is rescaled by L_C, the maximum possible length of care ($L_C = 25$ throughout), to express the length of care in time units.

Mated individuals produce a clutch and provide care for their offspring. During care, the A gene determines the allocation of care between two different tasks: a proportion of care A_s ($s = m, f$) is invested in task 1, while $(1 - A_s)$ is invested in task 2. The value of care, V, received by the clutch in time unit t is

$$V_t = B_1(A_m + A_f) + B_2[(1 - A_m) + (1 - A_f)] \\ + B_3\{(A_m + A_f)[(1 - A_m) + (1 - A_f)]\} \tag{1a}$$

while both parents care;

$$V_t = B_1 A_m + B_2(1 - A_m) + B_3 A_m(1 - A_m) \tag{1b}$$

while only the male cares; and

$$V_t = B_1 A_f + B_2(1 - A_f)B_3 A_f(1 - A_f) \tag{1c}$$

while only the female cares (fig. 3*A*).

Here B_1 and B_2 scale the effect of investment into tasks 1 and 2, respectively ($B_1 = B_2$ for all computations). Meanwhile, B_3 describes the synergistic effect of the investment; that is, if $B_3 > 0$, then investing into both tasks simultaneously improves the value of care nonadditively. In other words, if $B_3 > 0$, then the investment in one task is not interchangeable with the investment in the other. This may be the case when it is essential to perform both tasks; for instance, the young need both food and water or both food and grooming. The value $B_3 = 0$ can correspond to the case when a parent can choose between two equally suitable food sources. In this case, offspring survival is independent of the allocation of effort between tasks 1 and 2. Note, if $B_3 > 0$, then B_1 and B_2 are rescaled such that the benefit of care at equilibrium remains comparable with the case of $B_3 = 0$ (fig. 3*A*).

Care by an individual is terminated either when the individual decides to desert the clutch or when it dies. In cases of desertion, the length of care, L_s ($s = m, f$), is governed by the individual's L gene. This gene determines after how many time units spent in care the individual deserts the clutch. A deserting individual returns to the pool of singles and can mate again in the next time unit. We assume that neither parent cares more per time unit as compensation for its mate's desertion or death. The total value of the care, V_C, accumulates over the time units during which at least one parent cares for the clutch. When both parents have abandoned the clutch (for any reason), the young be-
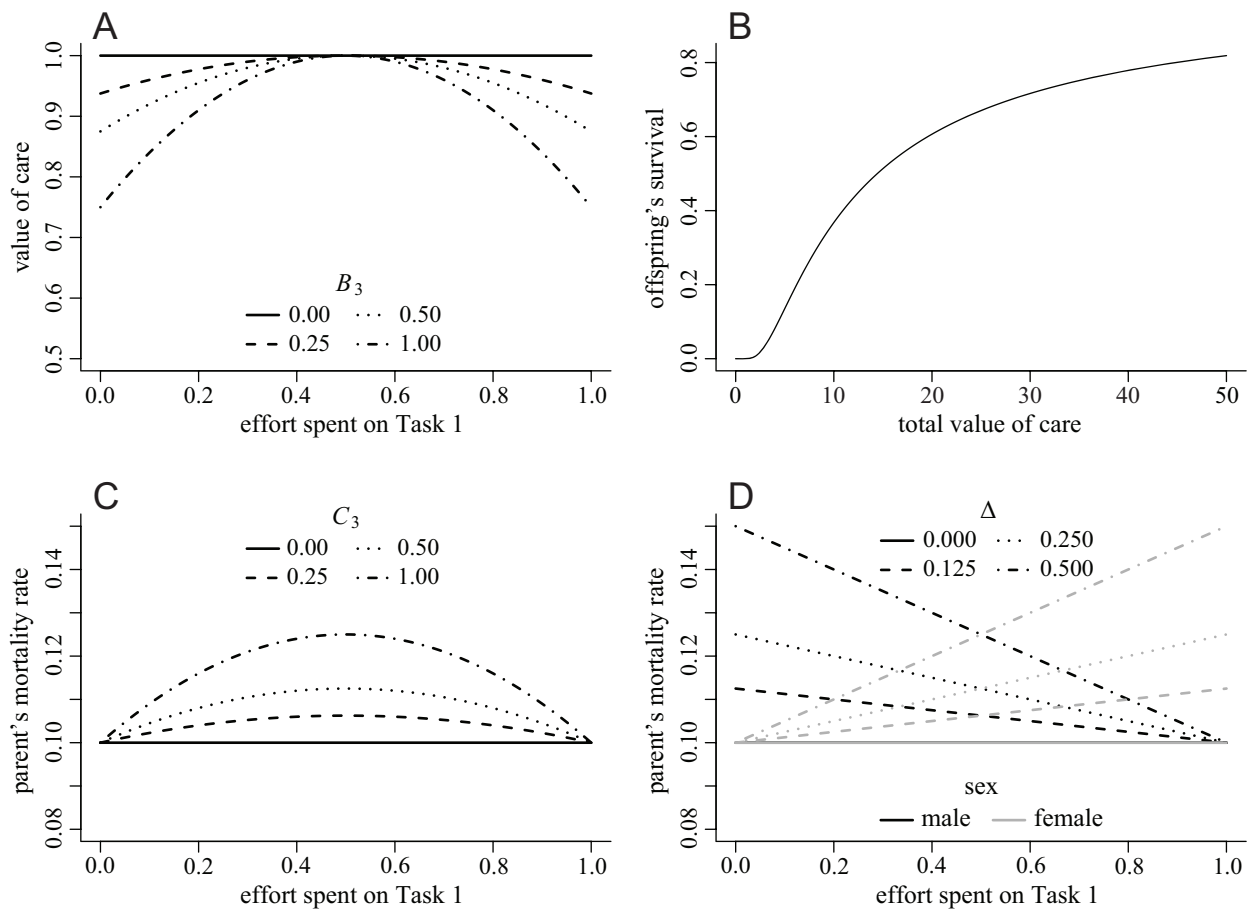
Figure 3: Assumptions of the model. *A*, The value of care over the allocation of parental effort to task 1 in one time unit. Effort invested in task 2 is $1 -$ effort invested in task 1. $B_3 > 0$ means that both types of care are required for offspring survival. The effect of B_3 is rescaled so that the maximum of the curve remains at the same value so the comparison of the runs is meaningful. *B*, The survival of offspring as the function of total care received during the entire period of care. *C*, The effect of synergistic cost on parental mortality rate. When $C_3 > 0$, there is an extra cost for investing in both tasks simultaneously. *D*, The implementation of skill difference (Δ). When $\Delta > 0$, the cost of task 1 exceeds that of task 2 by Δ for females, and the inverse is true for males. Parameter values for C_3 and Δ are chosen such that the mortality costs are comparable when the two tasks are performed simultaneously.

come independent. Their number ($n_{\text{fledglings}}$) depends on the clutch size (n_{young}), a parameter of the model, and the total value of care accumulated so far, as follows (fig. 3*B*; also see Kokko and Jennions 2008):

$$n_{\text{fledglings}} = n_{\text{young}} e^{-\alpha 2 L_C / V_C}. \tag{2}$$

Here L_C is applied to rescale the value of care into the 0–1 interval. The parameter α describes the shape of the relation. Because $n_{\text{fledglings}}$ is usually not an integer, the actual number of fledglings a pair produces is n_+ with probability P and n_- with probability $1 - P$, where n_+ is the smallest integer for which $n_+ > n_{\text{fledglings}}$, n_- is the largest integer for which $n_- < n_{\text{fledglings}}$, while $P = n_{\text{fledglings}} - n_-$. The sex ratio at fledging is $1 : 1$; that is, the probability that a male is produced is 0.5, while females are produced

with probability 0.5. During production of offspring, the parents' genome crossed over with probability 0.5, and mutation could change the value of any of the loci with probability 0.001. If mutation acts, then the value of the given locus changed by a random deviate drawn from a normal probability distribution with zero mean and SD is 0.05. The fledged young become members of the single pools and may mate in the next time unit.

Individuals may die at the end of the time units. Mortality has two components. One is the probability of background mortality, M_b, which is independent of the current behavior, while the other differs according to the state and sex of the individuals. The probabilities of mortality per unit time for single males and females are $M_{S,m}$ and $M_{S,f}$, respectively. The probability of mortality for an engaged

female, $M_{\text{E,f}}$, during a time unit depends on the allocation of investment between tasks, as follows:

$$M_{\text{E,f}} = \mu_{\text{C,f}} \times [C_1^{\text{f}} A_{\text{f}} + C_2^{\text{f}}(1 - A_{\text{f}}) + C_3^{\text{f}} A_{\text{f}}(1 - A_{\text{f}})] \quad (3a)$$

(mortality for an engaged male is similarly defined). Here $\mu_{\text{C,s}}$ is a parameter of the model, while C_1^s, C_2^s, and C_3^s describe the effect of allocation ($s = m, f$). If $C_1^s = C_2^s$ and $C_3^s = 0$, then there is no synergistic effect, and any kind of allocation between the two tasks is equivalent in terms of mortality cost (fig. 3C). If $C_3^s > 0$, then performing tasks simultaneously incurs higher mortality and hence should be avoided; that is, task specialization is expected (fig. 3C). Individuals should also specialize in one type of task if $C_3^s = 0$ but $C_1^s \neq C_2^s$; that is, an individual is more skilled at performing one task versus the other (fig. 3D). Consequently, the task that can be executed with less effort, that is, for which C_i^s ($i = 1, 2$) is smaller, should be preferred. Let us measure the level of skill differences by $\Delta^{\text{f}} = C_1^{\text{f}} - C_2^{\text{f}}$ for females and $\Delta^{\text{m}} = C_2^{\text{m}} - C_1^{\text{m}}$ for males (fig. 3D). Hereafter, we consider complementary skill differences as such that males and females mirror each other—that is, $\Delta^{\text{f}} = \Delta^{\text{m}}$—and we denote these skill differences with Δ. Note that at evolutionary equilibrium, the expected cost of care does not differ between the cases of $C_3^s = 0$, $\Delta = 0$, and $C_3^s > 0$ or $\Delta > 0$.

The actual mortality, M, also has a density-dependent component as follows:

$$M = (M_{\text{b}} + M_{St,s})^{1/(N/K)^{\delta}}, \quad (3b)$$

where subscript s is either m or f (i.e., male or female) and subscript St is either S or E (single or engaged). Value N is the actual population size, K is the carrying capacity of the environment, and δ scales the density-dependent effect.

To test how sex-based role specialization affects parental cooperation, we explore the effects of varying the synergistic benefit B_3, the synergistic costs C_3^s, and the degree of sex-based asymmetry in the cost of investing in tasks 1 and 2, Δ (fig. 3). To investigate the influence of sexual selection acting on males, we manipulated the variance in reproductive success of males relative to that of females. We also manipulated the degree of sex-biased mortality of caring parents. Each simulation started with 5,000 males and females whose genes were initialized independently of each other by a random number drawn from a uniform distribution between the limits of 0 and 1. Each simulation was run for 5×10^5 time units. At each time step, we measured the average length of care and the proportion of effort invested into task 1 for both sexes in the population.

Data and R code for the simulation and the figures presented here are deposited in the Dryad Digital Repos-itory: http://dx.doi.org/10.5061/dryad.h4g74 (Barta et al. 2014).

Effects of Synergistic Benefits, Costs, and Skill Differences

In the baseline case, all parameters are symmetric for the sexes (i.e., equal for males and females) and $B_3 = 1$ (i.e., both types of care are needed for the offspring). Further-more, we assume that C_3^s and Δ are all 0. Under this scenario, both sexes provide care (biparental care; fig. 4A) and both males and females invest into both types of care (no task specialization; fig. 4B). In this case, biparental care evolves because of the frequency-dependent effect generated by the Fisher condition: for members of the majority sex in the mating pool, it is more difficult to obtain a mate than for members of the minority sex; therefore, for the majority sex, it is more beneficial to provide care, everything else being equal (Kokko and Jennions 2008). This leads to an equalization of providing care. However, when sexual selection acts on males ($k_{\text{m}} > 1$, let us call this the baseline case with sexual selection), uni-parental care by females emerges (fig. 4C, 4D). The reason why females provide more care than males is because sex-ual selection favors successful males to focus on mate ac-quisition, and hence they can increase their reproductive success by providing little care.

Introducing skill differences ($\Delta = 0.5$; fig. 3D) in the case of baseline with sexual selection restores biparental care (fig. 4E). As strong sexual selection is acting on males, their intention is to desert the offspring soon after mating. But desertion forces the females to provide both types of care since offspring survival is the highest when they re-ceive both types of care. Because of the skill differences, this increases the mortality of caring females. The resulting lower number of single females in turn makes it more difficult for males to acquire a mate—a consequence of the Fisher condition. Therefore, the benefit of early de-sertion decreases, and males' best option becomes to pro-vide more care. This results in a more equal share of care by parents that allows each sex to begin to specialize, that is, to invest more into the task in which it is more efficient (fig. 4F). The appearance of task specialization, however, further increases the cost of desertion because a deserting parent leaves its offspring without one type of care when they need both of them. This makes biparental care more beneficial, which in turn leads to a higher degree of task specialization. This self-reinforcing process finally results in a population where stable biparental care is maintained by task specialization.

Introducing synergistic costs in the case of baseline with sexual selection produces results consistent with entering skill differences (results not shown). After desertion by the male, the female provides both types of care, which elevates
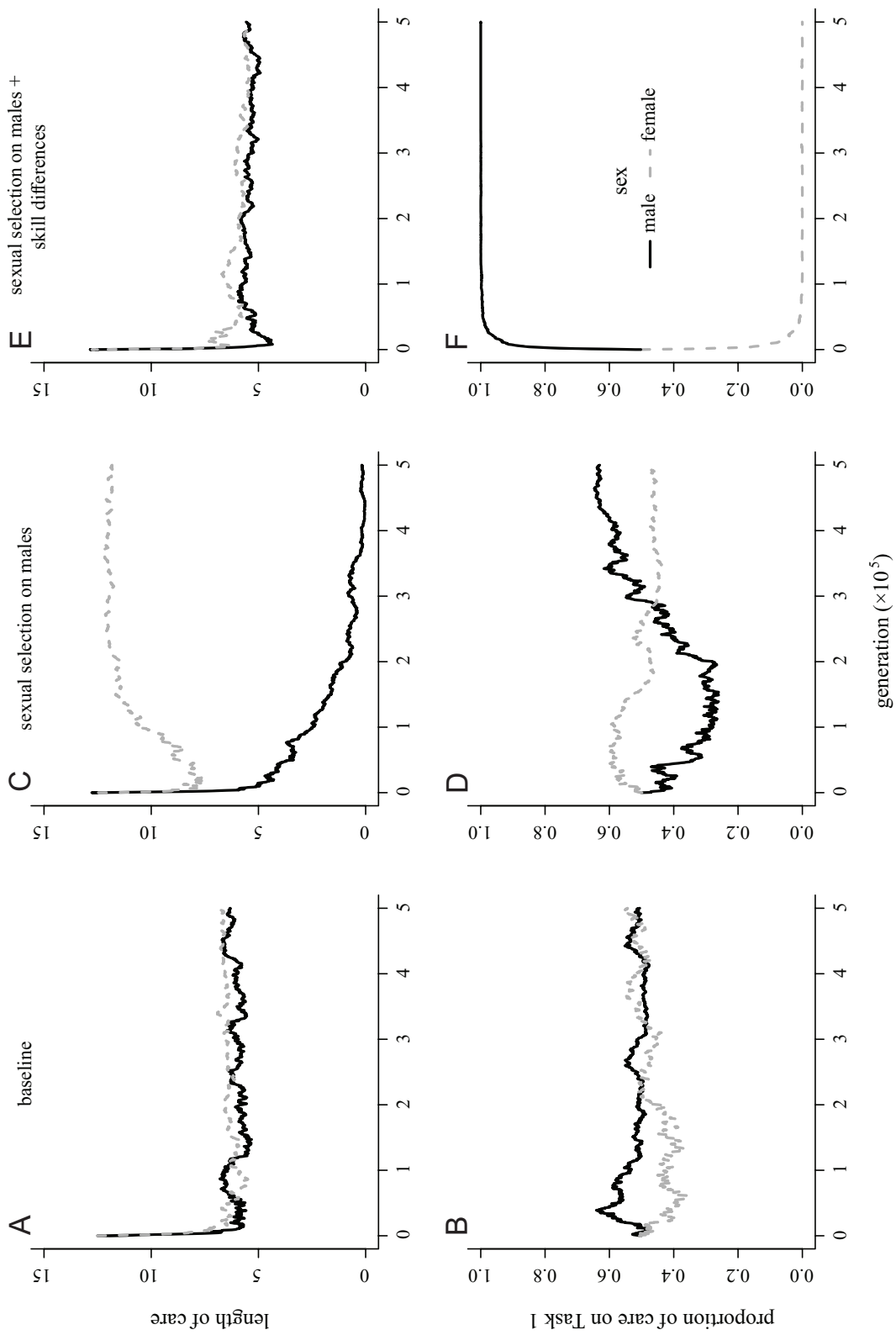
Figure 4: *A*, *B*, In the baseline case, males and females are identical and both C_3 and Δ equal 0. This results in biparental care with no sex-based task specialization. *C*, *D*, Sexual selection acting on males ($k_m = 5$) leads to uniparental care by females. *E*, *F*, Introducing skill differences ($\Delta = 0.5$) restores biparental care under sexual selection, leading to complete sex-based role specialization. Results of example runs are shown. Introducing synergistic costs has an analogous effect to skill differences (results not shown). $B_3 = 1$ throughout; for values of other parameters, see table 1.
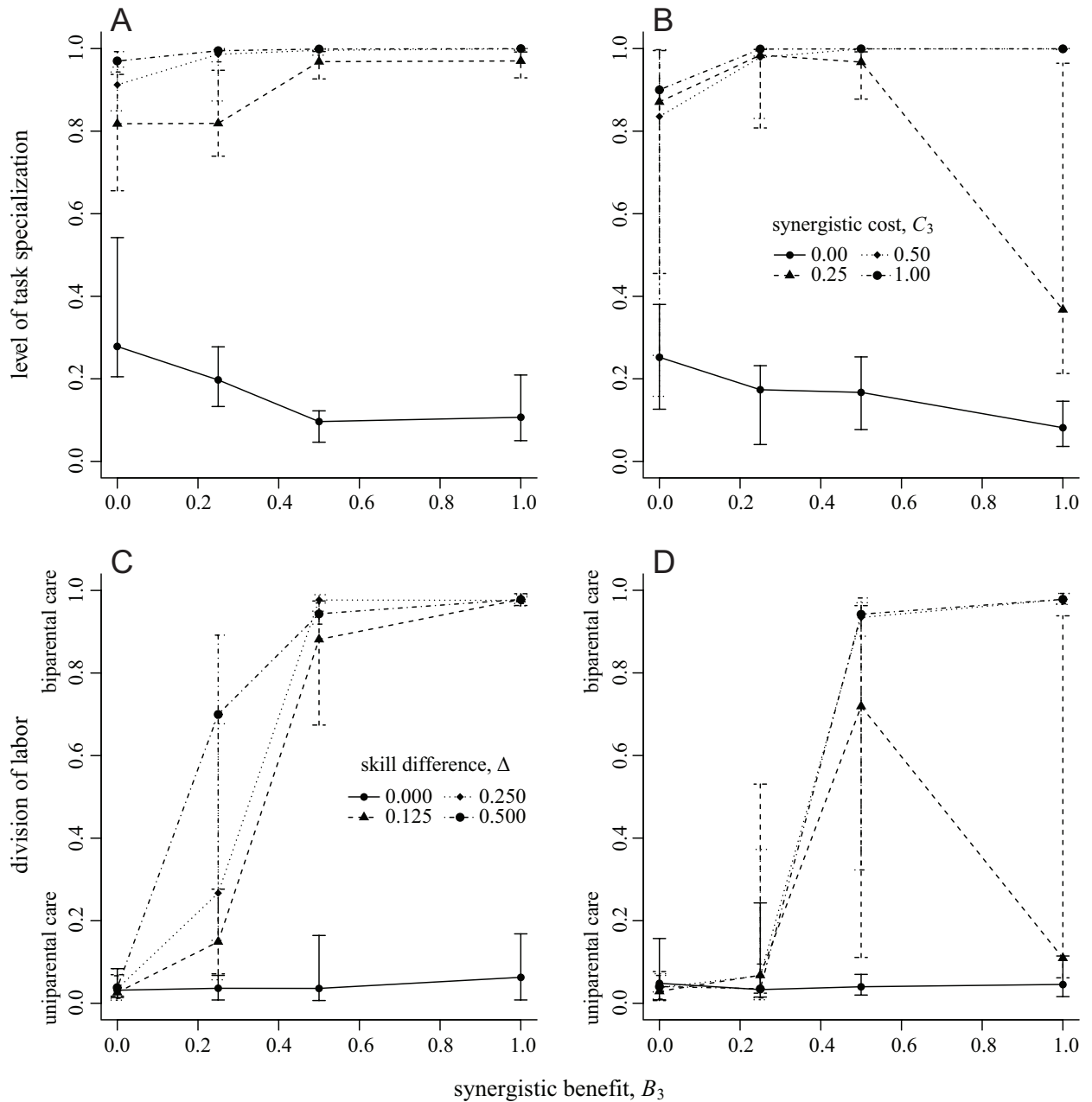
Figure 5: Skill differences ($\Delta > 0$; *A, C*) and synergistic cost ($C_3 > 0$; *B, D*) rapidly produce task specialization (*A, B*), whereas for equal division of labor (*C, D*) a synergistic benefit ($B_3 > 0$) is also required. The level of task specialization is given as $|(A_m - A_f)/(A_m + A_f)|$, where A_m and A_f are the effort invested in task 1 by males and females, respectively (note the effort invested in task 2 by sex s is $1 - A_s$). Division of labor is measured as $1 - |(L_m - L_f)/(L_m + L_f)|$, where L_m and L_f are the length of care provided by males and females, respectively. A_m, A_f, L_m, and L_f are genetically determined. Medians (symbols) and interquartile ranges (error bars) of 22 independent runs are given. For values of other parameters, see table 1.

her mortality because of the synergistic costs. This, through the Fisher condition, decreases the benefit of desertion, and so males remain to provide care; in this way, biparental care evolves. For reasons similar to those above, task spe-

cialization emerges. Because of the synergistic costs, both parents should avoid investing in both tasks equally, and hence they invest in one task. In addition, because of the synergistic benefits, the parents, given that both of them
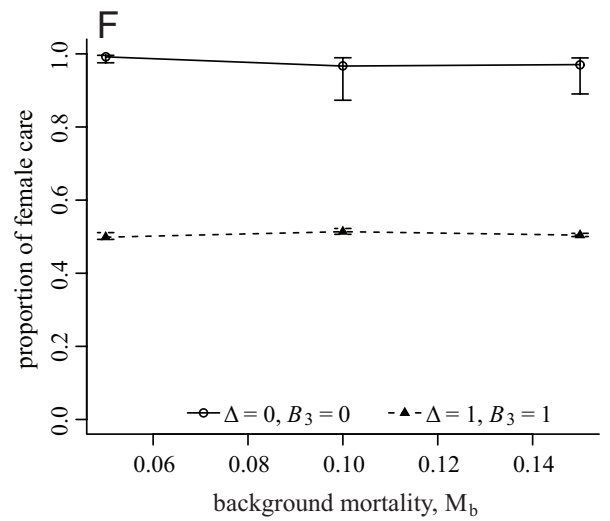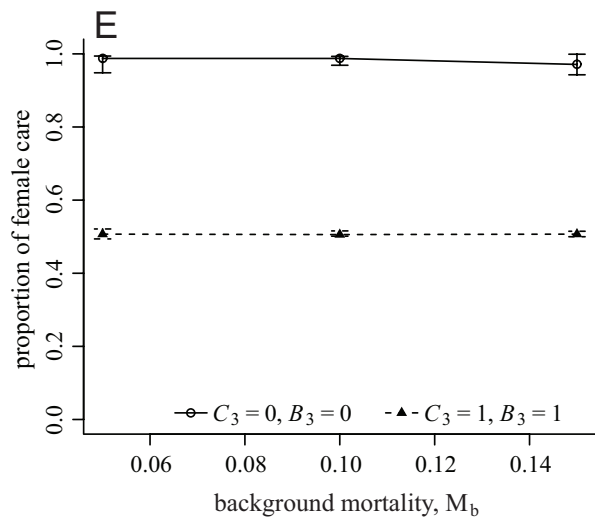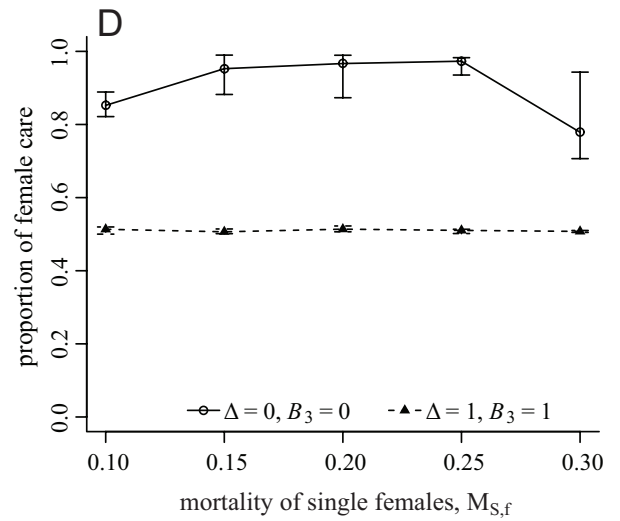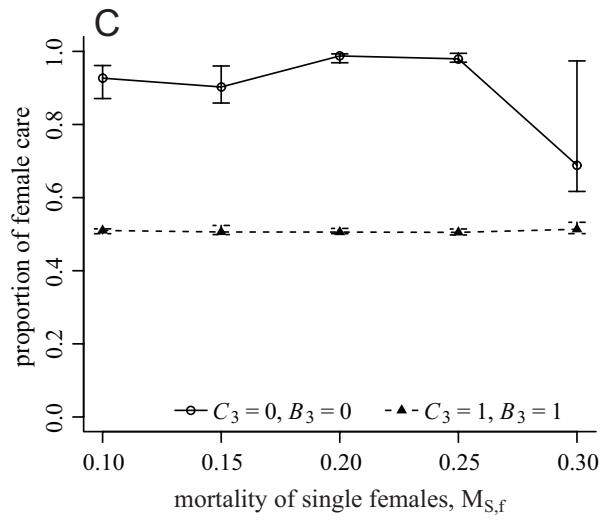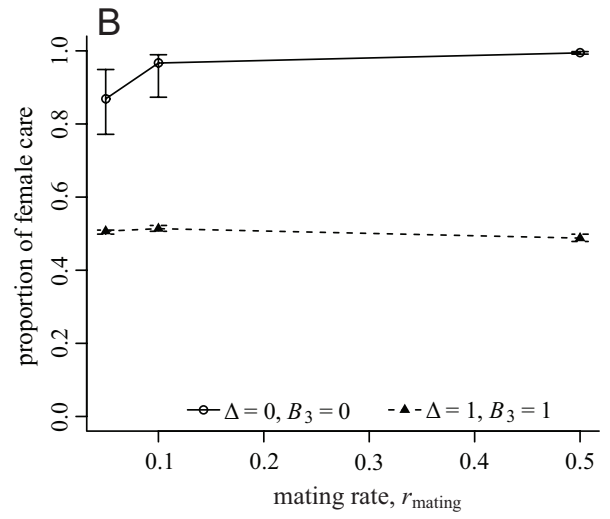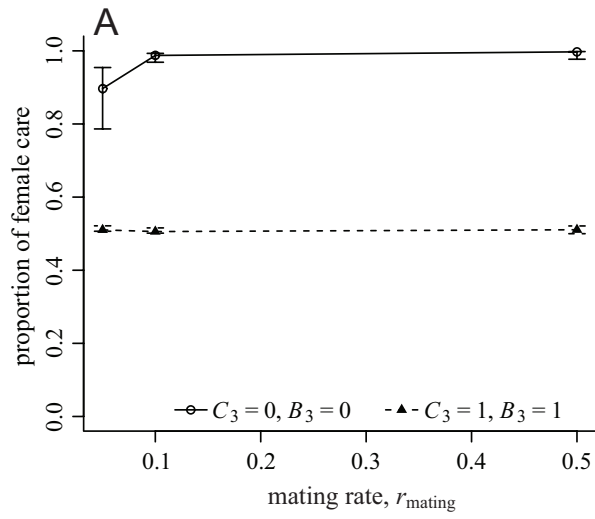
provide care, prefer to invest their efforts into different tasks; that is, if the male invests, let us assume, in task 1, then the female invests in task 2 or vice versa. As a result, a population with stable task specialization and stable biparental care evolves.

Systematic manipulation of B_3 with Δ or C_3^s shows that task specialization evolves even under small values of C_3^s ($C_3^s \geq 0.25$) or Δ ($\Delta \geq 0.125$), even when benefits are purely additive ($B_3 = 0$; fig. 5*A*, 5*C*). However, for the evolution of biparental care, an additional condition is required: B_3 should be relatively large ($B_3 > 0.25$); that is, tasks 1 and 2 should be functionally different for the offspring (fig. 5*B*, 5*D*). The latter result shows that two types of tasks facilitate biparental care only if both tasks are necessary for the success of the offspring (synergistic benefits) and either skill differences or synergistic costs make the simultaneous performance of the two tasks extra costly. Additional computations show that these results are robust to changes in mating rate, sex-specific mortality of single individuals, and background mortality (fig. 6).

Effects of Sexual Selection and Mortality Cost of Care

With increasing intensity of sexual selection on males, the proportion of male care decreases; that is, uniparental care by females evolves. However, the effects of synergistic benefits (i.e., offspring need both types of care) with the parents specializing in different tasks (either because of skill differences or synergistic costs) counteract even the effect of strong sexual selection, and biparental care remains for a large range of sexual selection (fig. 7*A*, 7*B*).

The mortality cost of parental care also influences the pattern of care. When the cost of care is equal for the sexes, both parents provide care. If the cost of mortality differs between the sexes, then the sex with lower mortality cares for the brood and the other parent deserts. Nevertheless, synergistic benefits and parental specialization may counteract the effect of mortality-cost differences, and care remains biparental for rather large mortality differences (fig. 7*C*, 7*D*).

Discussion

We used an evolutionary simulation to show that when offspring require two noninterchangeable types of care, the synergistic costs of performing both tasks, or sex-based asymmetry in the costs of performing the tasks, leads to

the emergence of task specialization and biparental care. It may be possible to test this prediction by exploring whether more equal division of care coevolves with task specialization across species that exhibit variation in both care division and task specialization; birds and insects are two groups that could lend themselves to this type of analysis. Our model also showed that task specialization makes biparental care more robust in the face of strong sexual selection or sex-biased mortality.

Our results highlight a potential limitation of previous theoretical work that considers care to be a univariate quantity: failing to take into account the multivariate nature of care may lead to overly restrictive predictions of the ecological or demographic conditions under which biparental care can be maintained. For instance, in their seminal paper, Kokko and Jennions (2008) establish that biparental care exists when males and females have the same demographic and life-history values, and uniparental care emerges if at least one parameter is different between male and female parents. Our model shows that this is not necessarily the case: if the sexes specialize into different tasks, then biparental care emerges even if the sexes differ considerably in demographic or ecological traits. Furthermore, in their influential paper, Gross and Sargent (1985), on the basis of a unidimensional parental care model, suggest that the evolution of parental care may have cyclical dynamics; that is, populations with biparental care can be invaded by deserters leading to uniparental care or no care. From these states, biparental care can then emerge again. Our results, however, suggest that if care is multidimensional, then the occurrence of cyclical dynamics is less likely.

It is difficult to determine whether the values we use for C_3^s and Δ are realistic, because remarkably few experimental studies have sought to determine whether the costs of different care activities differ for males and females or whether the costs of care behaviors combine nonadditively (Lormée et al. 2005). However, several observations suggest that the scenarios envisaged in our model are realistic. First, in birds, the cost of rewarming eggs is consistent with the costs of incubation and care behaviors that necessarily entail leaving the nest (e.g., defense and foraging) combining synergistically. Second, some traits that directly influence the efficiency with which an animal can undertake a care behavior are under sexually antagonistic selection; for instance, in species with large sexual size dimorphism, the costs of incubation, hunting, and defense

Figure 6: Effects of synergistic costs ($C_3 > 0$; *A*, *C*, *E*) and skill difference ($\Delta > 0$; *B*, *D*, *F*) on cooperation between parents are robust to changes in mating rate (*A*, *B*), sex-specific mortality of single individuals (*C*, *D*), and background mortality (*E*, *F*) when intense sexual selection acts on males (case of baseline with sexual selection; other parameters are as in table 1). Medians (symbols) and interquartile ranges (error bars) of 22 independent runs are given.
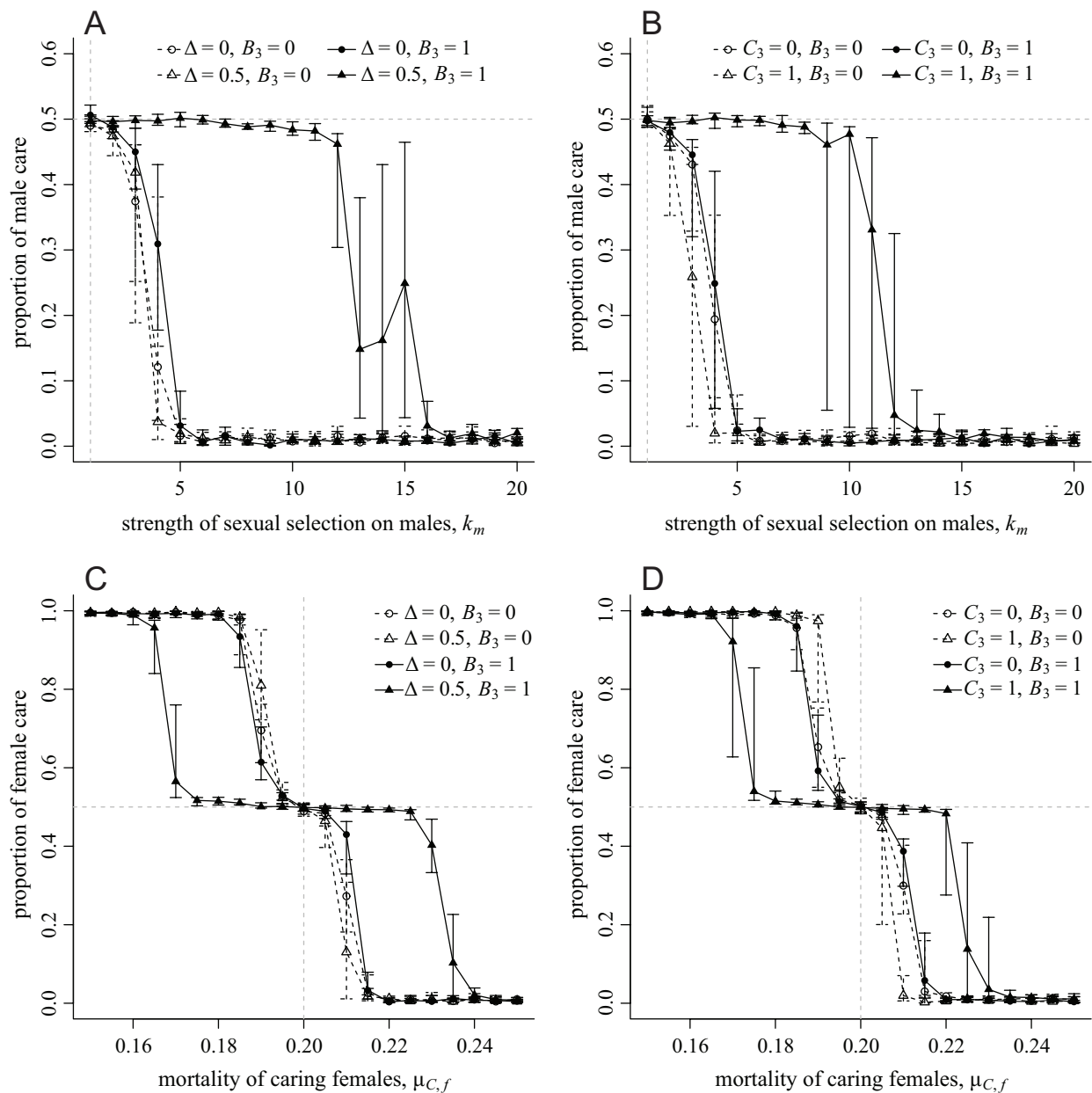
Figure 7: Increasing strength of sexual selection on males rapidly leads to desertion (no care) by males if B_3, Δ (*A*), or C_3^s (*B*) is zero. If there is a synergistic benefit ($B_3 > 0$) and skill differences ($\Delta > 0$; *A*) or a synergistic cost ($C_3^s > 0$; *B*), then biparental care is maintained even under strong sexual selection. The sex experiencing a higher level of mortality during parental care deserts while the other sex provides care if B_3 is zero and Δ (*C*) or C_3 (*D*) is zero. If there is a synergistic benefit ($B_3 > 0$) and either skill differences ($\Delta > 0$; *C*) or a synergistic cost ($C_3 > 0$; *D*), then biparental care is maintained even for large differences in sex-specific mortality. Vertical dashed lines mark the baseline cases (i.e., when there is no sexual selection or the mortality is equal for the two sexes), while horizontal dashed lines mark the equal division of labor. Medians (symbols) and interquartile ranges (error bars) of 22 independent runs are given.

are likely to be sex specific, as has been suggested for the co-occurrence of large sexual size dimorphism and care role specialization in raptors (Andersson and Norberg 1981). Third, in some biparental species, one sex displays specialized morphology or physiology related to care; for

example, in some altricial bird species, only one sex develops a brood patch. Finally, in burying beetles, males are both more likely than females to guard the nest and more effective than females at performing this task (Trumbo 2006). Future empirical work is needed to test (1) whether

the costs of performing specific care behaviors (as measured by loss of mass or condition) differ between males and females and (2) whether experimentally increasing investment in one type of care may lead to a greater than linear decrease in investment in a second care behavior.

Morphological and physiological specialization for care; that is, skill differences, however, may not necessarily result in biparental care. In placental mammals, for instance, only females develop elaborated machinery for gestation and lactation of the young, yet the predominant pattern in mammals is female-only care. A recent model (J. M. McNamara and M. Wolf, unpublished data) suggests that this can be the consequence of skill differences themselves evolving, a proposition that is not addressed in our model. It would be interesting to see what happens if differential costs can evolve under condition of multidimensional care. Patterns of care in humans, where males and females supply generally different resources to the offspring although fathers can contribute the majority of calories consumed by infants (Geary 2000), suggest that multidimensional care and specialization may maintain biparental care even in the face of evolving skill differences.

While we have specifically addressed the evolution of cooperation between parents, our results are consistent with the recently emerging view that within-population variation promotes cooperation in various contexts. Researchers have observed that behavioral diversity and concomitant division of labor increases the productivity of group-living spiders and ants (Modlmeier et al. 2012; Pruitt et al. 2012). Furthermore, behavioral variation and partner choice can enhance cooperation in standard game theoretic and market-based models (Noë and Hammerstein 1994; McNamara et al. 2004, 2008; Johnstone and Bshary 2008; Gavrilets 2012).

In our model, variation between individuals arose in two ways, both of which resulted in cooperation. First, it was a priori wired in by imposing skill differences between the sexes. Second, more importantly, role specialization, and hence variation, also spontaneously emerged when the sexes were alike, but simultaneous task performance was penalized. In biological market models (Noë and Hammerstein 1994; Johnstone and Bshary 2008), role specialization is assumed a priori, and modeling concentrates purely on how the relative frequencies of two specialized parties influence the maintenance of cooperation (the law of supply and demand; Noë and Hammerstein 1994). In contrast, in our model, task specialization evolves de novo and is then subject to market forces (e.g., feedback between single and caring individuals and density-dependent population regulation). Therefore, an important proposition emerging from our model is that the evolution of cooperation and role specialization are coevolutionary processes that reinforce each other. This means that not only

does variation promote cooperation, but the evolution of cooperation can generate variation. This parallels the work of Nonacs and Kapheim (2007), who point out that such a process, which they term "social heterosis," can facilitate the evolution of cooperation in the absence of close genetic relatedness and hence uniformity. Specialization and social heterosis thus provide an alternative route to cooperation that is distinct from kin selection (Hamilton 1964).

Many organisms rely on multiple types of cooperative behavior to exploit their environment, and animal societies commonly feature some degree of division of labor such that individuals specialize in different social roles (Oster and Wilson 1979; Ratnieks and Anderson 1999; Sugiyama and Sugiyama 2003; Arnold et al. 2005; Gazda et al. 2005). However, despite suggestions that social role variation may stabilize cooperation by increasing the interdependence of individuals or by increasing group productivity via efficient division of labor, it is interesting that the vast theoretical and empirical literature on the evolution of intraspecific cooperation (Székely et al. 2010; Bourke 2011) includes little explicit consideration of how the costs and benefits of investing in distinct cooperative behaviors interact and the implications this has for the coevolution of multiple social traits (also recently argued by McNamara 2013; see also Queller 1985). There is, however, one context in which cost trade-offs between different tasks have explicitly been invoked in social evolution. In his work on the evolution of multicellularity, Michod (2006) argues that convex curvature of the trade-off function between reproduction and viability (i.e., a synergistic cost of investing in both) is a prerequisite for germ-soma specialization and hence cooperation between cells. We note the parallel between this work and our model of cooperation over care. However, in contrast to the multilevel selection approach taken by Michod (2006) and a recent game-theoretic analysis of social role specialization (Boza and Számádó 2010), we show that social role specialization can promote the evolution of cooperation without the need to invoke group-level competition. We therefore propose the general hypotheses that synergistic costs and skill differences between two or more cooperative traits should confer a selective advantage to specialization, which in turn stabilizes cooperation over evolutionary time. A crucial step in testing whether our hypothesis can be extended to situations other than a care dilemma between two parents would be to see how relaxing the Fisher condition (i.e., having exactly two partners play the game) would alter our results.

In conclusion, we have considered two ways in which investment in discrete care behaviors can be linked: synergistic costs and sex-based cost asymmetry. We demonstrate that, when offspring require both types of care, synergistic costs or sex-based asymmetry lead to the evolution of sex-based care role specialization and the concomitant

stabilization of biparental care, even under strong sexual selection or sex-biased mortality. Aside from work on the evolution of multicellularity (Michod 2006), we are not aware of any other published work that explores the consequences of synergistic or asymmetric costs for the evolution of cooperation. While several authors (e.g., Nonacs and Kapheim 2007; Lessells 2012) have made verbal arguments that specialization should stabilize biparental care (or cooperation in general), numerical explorations of how and to what extent this can occur appear to be lacking from the literature. Thus, our model contributes to social evolution theory by (*a*) providing a specific process—task specialization—by which cooperation may arise, (*b*) showing that synergistic costs are as important as synergistic benefits, and (*c*) showing that task specialization and cooperation can coevolve. Therefore, the multidimensionality of many behavioral traits and resultant role specialization may be significant and currently not fully appreciated facilitators of social evolution.

Acknowledgments

Literature Cited

Alonzo, S. H. 2010. Social and coevolutionary feedbacks between mating and parental investment. Trends in Ecology and Evolution 25:99–108.

———. 2012. Sexual selection favors male parental care, when females can choose. Proceedings of the Royal Society B: Biological Sciences 279:1784–1790.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.

Andersson, M., and R. A. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. Biological Journal of the Linnean Society 15:105–130.

Arnold, K. E., I. P. F. Owens, and A. W. Goldizen. 2005. Division of labour within cooperatively breeding groups. Behaviour 142:1577–1590.

Barta, Z., A. I. Houston, J. M. McNamara, and T. Székely. 2002. Sexual conflict about parental care: the role of reserves. American Naturalist 159:687–705.

Barta, Z., T. Székely, A. Liker, and F. Harrison. 2014. Data from: Social role specialization promotes cooperation between parents. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.h4g74.

Bourke, A. F. G. 2011. Principles of social evolution. Oxford University Press, Oxford.

Boza, G., and S. Számadó. 2010. Beneficial laggards: multilevel selection, cooperative polymorphism and division of labour in threshold public good games. BMC Evolutionary Biology 10:336.

Clutton-Brock, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, NJ.

Clutton-Brock, T. H., and G. A. Parker. 1992. Potential reproductive rates and the operation of sexual selection. Quarterly Review of Biology 67:437–456.

Cockburn, A. 2006. Prevalence of different modes of parental care in birds. Proceedings of the Royal Society B: Biological Sciences 273:1375–1383.

Deeming, D. C. 2002. Avian incubation: behaviour, environment, and evolution. Oxford University Press, Oxford.

Gavrilets, S. 2012. Human origins and the transition from promiscuity to pair-bonding. Proceedings of the National Academy of Sciences of the USA 109:9923–9928.

Gazda, S. K., R. C. Connor, R. K. Edgar, and F. Cox. 2005. A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. Proceedings of the Royal Society B: Biological Sciences 272:135–140.

Geary, D. C. 2000. Evolution and proximate expression of human paternal investment. Psychological Bulletin 126:55–77.

Grafen, A., and R. Sibly. 1978. A model of mate desertion. Animal Behaviour 26:645–652.

Gross, M. R., and R. C. Sargent. 1985. The evolution of male and female parental care in fishes. American Zoologist 25:807–822.

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

Harrison, F., Z. Barta, I. Cuthill, and T. Székely. 2009. How is sexual conflict over parental care resolved? a meta-analysis. Journal of Evolutionary Biology 22:1800–1812.

Houston, A. I., T. Székely, and J. M. McNamara. 2005. Conflict between parents over care. Trends in Ecology and Evolution 20:33–38.

———. 2013. The parental investment models of Maynard Smith: a retrospective and prospective view. Animal Behaviour 86:667–674.

Johnstone, R. A., and R. Bshary. 2008. Mutualism, market effects and partner control. Journal of Evolutionary Biology 21:879–888.

Johnstone, R. A., and C. A. Hinde. 2006. Negotiation over offspring care: how should parents respond to each other's efforts? Behavioral Ecology 17:818–827.

Kokko, H., and M. Jennions. 2008. Parental investment, sexual selection and sex ratios. Journal of Evolutionary Biology 21:919–948.

Lessells, C. M. 1999. Sexual conflict in animals. Pages 75–99 *in* L. Keller, ed. Levels of selection in evolution. Princeton University Press, Princeton, NJ.

———. 2012. Sexual conflict. Pages 150–170 *in* N. J. Royle, P. T. Smiseth, and M. Kölliker, eds. The evolution of parental care. Oxford University Press, Oxford.

Lormée, H., C. Barbraud, and O. Chastel. 2005. Reversed sexual size dimorphism and parental care in the red-footed booby *Sula sula*. Ibis 147:307–315.

Maynard Smith, J. 1977. Parental investment: a prospective analysis. Animal Behavior 25:1–9.

McGraw, L., T. Székely, and L. J. Young. 2010. Pair bonds and parental behaviour. Pages 271–301 *in* T. Székely, A. Moore, and J. Komdeur, eds. Social behaviour: genes, ecology and evolution. Cambridge University Press, Cambridge.

McNamara, J. M. 2013. Towards a richer evolutionary game theory. Journal of the Royal Society Interface 10:20130544.

McNamara, J. M., Z. Barta, L. Fromhage, and A. I. Houston. 2008. The coevolution of choosiness and cooperation. Nature 451:189–192.

McNamara, J. M., Z. Barta, and A. I. Houston. 2004. Variation in behavior promotes cooperation in the prisoner's dilemma game. Nature 428:745–748.

McNamara, J. M., C. E. Gasson, and A. I. Houston. 1999. Incorporating rules for responding into evolutionary games. Nature 401:368–371.

McNamara, J. M., A. I. Houston, Z. Barta, and J. L. Osorno. 2003. Should young ever be better off with one parent than two? Behavioral Ecology 14:301–310.

McNamara, J. M., T. Székely, J. N. Webb, and A. I. Houston. 2000. A dynamic game-theoretic model of parental care. Journal of Theoretical Biology 205:605–623.

Michod, R. E. 2006. The group covariance effect and fitness trade-offs during evolutionary transitions in individuality. Proceedings of the National Academy of Sciences of the USA 103:9113–9117.

Modlmeier, A. P., J. E. Leibmann, and S. Foitzik. 2012. Diverse societies are more productive: a lesson from ants. Proceedings of the Royal Society B: Biological Sciences 279:2142–2150.

Motro, U. 1994. Evolutionary and continuous stability in asymmetric games with continuous strategy sets: the parental investment conflict as an example. American Naturalist. 144:229–241.

Noë, R., and P. Hammerstein. 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. Behavioral Ecology and Sociobiology 35:1–11.

Nonacs, P., and K. M. Kapheim. 2007. Social heterosis and the maintenance of genetic diversity. Journal of Evolutionary Biology 20:2253–2265.

Oster, G. F., and E. O. Wilson. 1979. Caste and ecology in the social insects. Princeton University Press, Princeton, NJ.

Owens, I. P. F., and P. M. Bennett. 1994. Mortality costs of parental care and sexual dimorphism in birds. Proceedings of the Royal Society B: Biological Sciences 257:1–8.

Pruitt, J. N., C. E. Oufiero, L. Avilés, and S. E. Riechert. 2012. Iterative evolution of increased behavioral variation characterizes the transition to sociality in spiders and proves advantageous. American Naturalist 180:496–510.

Queller, D. C. 1985. Kinship, reciprocity and synergism in the evolution of social behavior. Nature 318:366–367.

Ratnieks, F. L. W., and C. Anderson. 1999. Task partitioning in insect societies. Insectes Sociaux 46:95–108.

Reynolds, J. D., N. B. Goodwin, and R. P. Freckleton. 2002. Evolutionary transitions in parental care and live bearing in vertebrates. Philosophical Transactions of the Royal Society B: Biological Sciences 357:269–281.

Royle, N. J., P. T. Smiseth, and M. Kölliker. 2012. The evolution of parental care. Oxford University Press, Oxford.

Sugiyama, L., and M. Sugiyama. 2003. Social roles, prestige, and health risk. Human Nature 14:165–190.

Székely, T., T. Lislevand, and J. Figuerola. 2007. Sexual size dimorphism in birds. Pages 27–37 *in* D. Fairbairn, W. Blanckenhorn, and T. Székely, eds. Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford.

Székely, T., A. J. Moore, and J. Komdeur. 2010. Social behaviour: genes, ecology and evolution. Cambridge University Press, Cambridge.

Székely, T., V. Remeš, R. P Freckleton, and A. Liker. 2013. Why care? inferring the evolution of complex social behaviour. Journal of Evolutionary Biology 26:1381–1391.

Tallamy, D. W. 2001. Evolution of exclusive paternal care in arthropods. Annual Review of Entomology 46:139–165.

Trillmich, F. 2010. Parental care: adjustments to conflict and cooperation. Pages 267–298 *in* P. Kappeler, ed. Animal behaviour: evolution and mechanisms. Springer, Heidelberg.

Trivers, R. 1972. Parental investment and sexual selection. Pages 136–179 *in* B. Campbell, ed. Sexual selection and the descent of man. Aldine, Chicago.

Trumbo, S. T. 2006. Infanticide, sexual selection and task specialization in a biparental burying beetle. Animal Behaviour 72:1159–1167.

———. 2012. Patterns of parental care in invertebrates. Pages 81–100 *in* N. J. Royle, P. T Smiseth, and M. Kolliker, eds. The evolution of parental care. Oxford University Press, Oxford.

Yamamura, N., and N. Tsuji. 1993. Parental care as a game. Journal of Evolutionary Biology 6:103–127.