Relative fitness of alternative male reproductive tactics in a mammal varies between years

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Summary

1. In many species, males can use different behavioural tactics to achieve fertilization, so-called alternative reproductive tactics (ARTs). Few field studies have measured fitness consequences of ARTs under varying environmental conditions.

2. Here, we describe fitness consequences of three phenotypically plastic ARTs in the African striped mouse (*Rhabdomys pumilio*) and show that relative fitness of ARTs differs between years. Each year represents a different generation.

3. For the generation living under high population density, tactics differed in relative fitness in accordance with the theory of conditional strategies, with highly successful territorial breeding males having 10 times higher success than solitary roaming males and 102 times higher success than adult natally philopatric males.

4. For the generation living under intermediate population density, the territorial breeding and roaming tactics yielded similar fitness, which would be in agreement with the theory of mixed strategies. No philopatric males occurred.

5. For the generation living under low population density, roaming was the only tactic used and some roamers had very high fitness.

6. The main prediction of status-dependent selection for conditional strategies is a correlation between fitness and status, often measured as body mass, but we did not find this correlation within tactics when more than one tactic was expressed in the population.

7. Female distribution seems to have an effect on which reproductive tactics male chose: female defence polygyny when females are clumped (interference competition), but a searching tactic when females are dispersed (scramble competition). In contrast to predictions arising from theory on scramble competition, male body mass was important in determining fitness only in the year when females were dispersed, but not in other years.

8. Our results indicate that the differentiation between conditional and mixed strategies is not an absolute one. In many other species, environmental conditions might fluctuate temporally and spatially so that the normally suboptimal tactic yields similar fitness to the (usually) dominant tactic or that only a single tactic prevails.

9. We suggest the term single strategy, independent of current fitness consequences, for systems where tactics are not genetically determined, in contrast to genetically determined alternative strategies.

Key-words: female choice, prairie vole, scramble competition, social flexibility

Introduction

Reproductive tactics of males are influenced by the spatial distribution of females, with a clumped distribution favouring harem defence polygyny (interference competition), and a dispersed distribution favouring a male searching tactic (scramble competition; Emlen & Oring 1977; Lane *et al.* 2009; Shuster & Wade 2003). However, individual males can differ in their reproductive tactics to maximize fitness. Such alternative reproductive tactics (ARTs) have been described in vertebrates and invertebrates, and they are more common in males than in females (Taborsky, Oliveira & Brockmann

2008). While ARTs have been reported for more than 100 species, fitness consequences have been measured in only a few species, most often with genetically determined ARTs (e.g. Lank *et al*. 1995; Shuster & Sassaman 1997). We still know relatively little about how ARTs do or do not differ in fitness, which is critical to understanding how they evolved and how they are maintained (Taborsky, Oliveira & Brockmann 2008).

Alternative reproductive tactics are the result of underlying strategies. A strategy describes the decision rules of an individual, whereas a tactic is the behaviour resulting from these decision rules (Krebs & Davies 1993). Gross (1996) defined three different strategies. In alternative strategies, ARTs are genetically polymorphic and different tactics yield the same average fitness. Such genetically determined ARTs have been documented in fish (Taborsky 2008a), lizards (Moore, Hews & Knapp 1998), ruffs (*Philomachus pugnax*; Lank *et al*. 1995) and the isopod *Paracerceis sculpta* (Shuster & Sassaman 1997). In contrast, in mixed strategies, individuals are able to express all tactics. Crucially, alternative and mixed strategies are both characterized by frequency-dependent selection resulting in equal fitness between tactics. However, to our knowledge, no convincing example for a mixed strategy has been found (Gross 1996). In most cases, different tactics are believed to differ in fitness and are based on conditional strategies (Gross 1996). In species with conditional strategies, the tactic that an individual chooses depends on its competitive abilities, leading to status-dependent selection. The most competitive individuals follow the tactic that yields the greatest fitness pay-off, called the bourgeois tactic. Less-competitive males, which are often smaller and younger than the bourgeois males, make the best of a bad job (Dawkins 1980), following a tactic (often called sneaker or satellite) with low fitness that is still better than no reproductive success at all. These males change to the bourgeois tactic when they grow larger. To understand the evolution of ARTs, it is crucial to understand the fitness pay-offs of the different tactics to predict when and why individuals change their tactic: when do fitness functions of different tactics cross, such that a switch-point from one tactic to another is reached (Taborsky 2008b)?

Males of the African striped mouse (*Rhabdomys pumilio*) follow one of the three ARTs: group living territorial breeder, group living natally philopatric male or solitarily living roaming male. Males can switch tactics during their lives (Schradin *et al*. 2009). Relative body mass appears to determine tactic as philopatric males are small, roaming males are intermediate in mass and territorial breeders are the heaviest. Upon gaining mass, philopatrics can change into roamers or territorial breeders, and roamers can become territorial breeders (Schradin *et al*. 2009). Males also follow alternative dispersal tactics, with larger males dispersing over shorter distances, smaller males often being forced to disperse large distances over suboptimal habitat (Solmsen, Johannesen & Schradin 2011). Males typically remain natally philopatric during the breeding season they are born and have the chance to reproduce as roamers or territorial males during the next

breeding season. They gain weight the season they are born and the winter preceding the next breeding season, when it rains and plant growth occurs. Large philopatrics might immigrate into groups that lost their breeding male (e.g. because of predation) any time of the year. Males that remained philopatric until the start of the next breeding season then might either remain philopatric or become roamers, and during the breeding season, males can switch tactic as their body mass increases (Schradin *et al*. 2009). However, adults experience only one breeding season; therefore, they cannot delay reproduction to another year when they might be heavier. This also means that every year of field study investigates a new generation.

We predict that fitness in the striped mouse is status (condition) dependent, with breeders having the highest fitness, roamers intermediate fitness and philopatrics the lowest fitness. We also predict that within tactics, fitness depends on body mass (status-dependent selection) because heavier males are more likely to win male–male competitions (Schradin 2004) and male body mass is known to be important in other polygynous mammals (Heske & Ostfeld 1990; Adrian *et al*. 2008). We expect that territorial breeder and roamer-specific fitness functions intersect, at a switch-point located between the mean body mass for territorial breeders and roamers (Fig. 1a).

One of the most interesting features of ARTs of the African striped mouse is that they vary with environmental conditions. The three tactics co-occur when population density is high. However, in a year with very low population density when females were dispersed as single breeders, all males followed the roaming tactic (Schradin, König & Pillay 2010). Under such environmental conditions, one would expect scramble competition and selection favouring traits like search ability and not body mass. Additionally, as single breeding females are a valuable resource, large roamers might be better able to monopolize them during the day of oestrus such that body mass and fitness would be positively correlated (Fig. 1c).

At intermediate population density, both solitary and communally breeding females occur as well as territorial breeding and roaming males but no adult philopatric males are present in the population. Importantly, under these conditions, roaming and territorial males do not differ in body mass. If body mass is a good proxy of competitive ability, and males were thus not differing in status, we predict that roaming and territorial males do not differ in reproductive success under these specific environmental conditions. We still expect fitness to be dependent on body mass, as heavier males should be more successful in male–male competition (Fig. 1b).

The tactic that male striped mice follow depends on population density (Schradin, König & Pillay 2010). In the current study, we choose 3 years differing strongly in population density to test theoretical assumptions of the fitness consequences for different tactics. We therefore test whether the fitness functions of male African striped mice correspond to predictions arising from status-dependent selection.
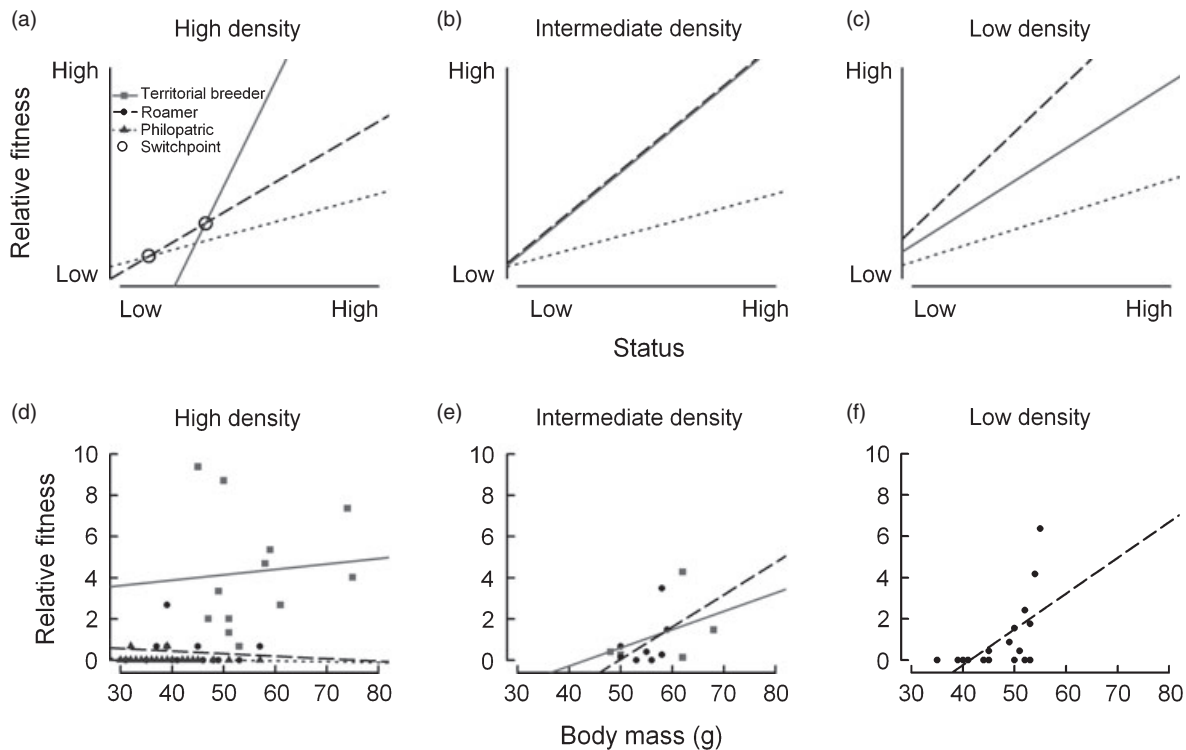
Fig. 1. (a–c) Predictions arising from status-dependent selection (derived from Fig. 1.3. in Taborsky, Oliveira & Brockmann 2008). For each year, we predicted fitness to be dependent on body mass (status), i.e. that heavier males were more successful. (a) Under high population density, heavy males were predicted to follow the tactic of territorial breeder, giving the highest fitness, intermediate mass males to be solitary roamers with intermediate fitness and small males to be philopatrics with low fitness. Predicted switch-points are marked. (b) Under intermediate population density when territorial breeders and roamers did not differ in body mass, we predicted the fitness functions for roamers and territorial breeders to be identical, and the fitness line of philopatrics is always below the other lines. No switch-points occur. (c) Under low population density, the fitness line for roamers is always above the lines for territorial breeders and philopatrics. No switch-points occur. (d–f) Results. Least-square linear fits of mass vs. relative fitness for tactics occurring each year. (d) Territorial breeders had higher fitness than roamers and philopatrics had the lowest fitness, but fitness did not increase with mass. The slopes of these regressions are not significantly different from zero (territorial breeding males: $t_{1,10} = 0.28$, $P > 0.78$; roamers: $t_{1,13} = 0.45$, $P > 0.66$; philopatrics: $t_{1,30} = 0.80$, $P > 0.42$). (e) No philopatrics were present. Territorial breeders had similar fitness to roamers, but fitness did not increase with body mass. Neither regression was significant (territorial breeding males: $t_{1,3} = 0.84$, $P > 0.46$; roamers: $t_{1,6} = 1.31$, $P > 0.23$). (f) Only one tactic occurred. Body mass predicted fitness ($t_{1,16} = 2.96$, $P < 0.01$).

Materials and methods

STUDY AREA AND PERIOD

The study was conducted in the Goegap Nature Reserve in South Africa (S 29 41.56, E 18 1.60). The vegetation type is Succulent Ka-roo, an arid area, with an average rainfall of 160 mm p.a. Most rain occurs in autumn/winter from April until July, some rain falls in spring (August/September), while summer (December–March) is the dry season.

Data were collected during 1 year with very low population density (2003: 1·5 mice ha^{-1}), 1 year with intermediate population density (2007: 6·5 mice ha^{-1}) and 1 year with high population density (2005: 19·0 mice ha^{-1}). The low population density in 2003 was because of an extreme winter drought and is the year with the lowest population density in our long-term study, but represents the condition found in other habitats with low population density (Schradin & Pillay 2005b). In 2003, all females were breeding solitarily, and in 2005 all females were breeding in communal groups, while in 2007 both communal groups and solitary breeding females occurred (Table 1). The size of the study area changed from 16·0 ha in 2003 to 8·8 ha in 2005 to 7·4 ha in 2007.

STUDY SPECIES

Striped mice are diurnal, inhabit an open habitat and are readily habituated to the presence of observers, which allows direct behavioural observations in the field (Schradin 2006). The breeding season of 3–4 months occurs in spring and depends on rainfall (Schradin & Pillay 2005a). In the current study, breeding took place from September to December in 2003, and from August to November during the years 2005 and 2007.

DETERMINATION OF MALE TACTICS

In our study, we considered all males with a body mass above 30 g and that were older than 4 weeks as reproductively mature (Brooks 1982). Male tactics were determined by a combination of trapping, behavioural observations and radiotracking (for sample sizes, see Table 1). Trapping was done around nesting sites at least 3 days per month. Trapped mice were weighed and sexed; males were recorded as scrotal (testes descended) or not (testes inside the body), and all mice were permanently marked with ear tags (National Band and Tag Co., Ontario, USA) and hair dye (Rapido, Pinetown, South Africa) for individual recognition during behavioural observations.

Table 1. Demographic descriptors of the study population and sample sizes for paternity studies during the three study years

Population density (striped mice per ha)	Year	Number of single females	Number of groups of communally breeding females	Sex ratio (males : females)	Ratio adult males : communally breeding female groups	Offspring	Litters > 1 pup	Philopatric males present at start of breeding season	Philopatric males born during breeding season	Roamers	Territorial breeders	Neighbouring males (tactic unknown)
19·0	2005	0	10	2·7	5·6	125	24	32 (55%)	41	15 (25%)	12 (20%)	10
6·5	2007	10	7	0·7	1·9	105	24	0 (0%)	0	8 (62%)	5 (38%)	0
1·5	2003	9	0	1·1	0·0	89	28	0 (0%)	46	18 (100%)	0 (0%)	0

Each nest was observed for 2–3 days in a row both during mornings and afternoons for 45 min at least every 2 weeks to determine group composition.

All territorial breeders and roamers were equipped with MD-2C radiotransmitters (Holohil, Canada) and radiotracked as described elsewhere (Schradin & Pillay 2005b) to determine home ranges (data presented in Schradin *et al.* 2009) and sleeping sites. Not all philopatrics (which only occurred in 2005) were radiocollared, as their tactic could be reliably determined by behavioural observations at their natal nests.

We classified males as philopatric if they had been trapped as juveniles (< 30 g) at a specific group and were as adults observed at the same group. Roaming males were classified as adult males that did not permanently share nesting sites with any other mice, although they might have spent some nights with single breeding females. Territorial breeding males were adult males that lived in groups other than their natal group. The latter were always the heaviest males of the groups, and each communal group had only one territorial breeding male. Males could only show one tactic at a time, i.e. they were either radiotracked > 50% of the time sleeping alone (roamers), or > 60% of the time sleeping with one group that was not their natal group (territorial breeders), or they were only trapped and observed at their natal group (philopatrics).

PATERNITY ANALYSIS

Through extensive trapping, we were able to obtain tissue samples (tail clips) for genetic analyses from all juveniles observed at the field site and from every observed adult male and female (Table 1). We isolated DNA from mouse tissue using magnetic particle purification (BioSprint 96 DNA Blood kit; Qiagen, Newport, KY, USA). We used nine polymorphic microsatellite loci from the house mouse genome (Teschke *et al.* 2008) and amplified them using two multiplexes. Both the first (Chr13_1, Chr1_12, Chr1_21, Chr2_3, Chr7_64) and the second multiplex (D3Mit211, Chr11_81, Chr19_18, Chr5_38) were amplified using the Qiagen PCR Multiplex kit with a final concentration of 0·1/0·2 μM primer for 35 cycles at an annealing temperature of 60 °C. Mean number of alleles per locus was 16·8 ± 4·3 (SD). In each year, one locus was identified in Cervus as being out of Hardy–Weinberg equilibrium, but the identity of the locus was different each time, so we retained all loci for parentage analysis. Typing error rates were estimated by amplifying and genotyping 153 individuals at the nine loci twice and calculated as the number of alleles that were scored differently between the two PCR amplifications divided by the total number of scored alleles. The observed error rate of 0·014 was strongly influenced by poor repeatability of amplification of one locus in one 96-well plate; if this one plate was excluded from the average, the average error rate then fell below 0·01.

Parentage analyses were performed separately for each year using Cervus 3.0 (Kalinowski, Taper & Marschall 2007). Parameters for the simulation of parentage analysis were set as 100 000 offspring, 95% sampling of candidate mothers, 85% sampling of candidate fathers (to be conservative), 0·015 proportion of loci mistyped (to be conservative) and the confidence level was set at a conservative 95%. Proportion of loci typed was 0·988 (2003), 0·975 (2005) and 0·978 (2007). We accepted parentage assignment when trio confidence was 95% and there was zero or one mismatch between each parent and offspring, and no more than two mismatches in the trio of candidate parents and offspring. If trio confidence was less than 95% but a parent–offspring pair met the 95% confidence threshold with one or fewer mismatches, we accepted the maternity

or paternity. If both a mother and father of the same offspring could be separately assigned with 95% confidence and one or fewer pair mismatches, but the trio had a confidence value of less than 95% and/or had more than two trio mismatches, we awarded parentage to the putative father if its pair delta value with the offspring exceeded that of the putative mother, and *vice versa*. Success in maternity assignment was 82·0% in 2003, 84·0% in 2005 and 97·1% in 2007. Success in paternity assignment was 92·4% in 2003, 78·0% in 2005 and 93·3% in 2007.

INFLUENCE OF THE SIRE'S TACTIC ON HIS SON'S TACTIC?

In total, we had 155 sons, of which 24 were still present as adults at our field site the next breeding season. We determined the reproductive tactic of these males as adults. Sample sizes were too low to directly estimate heritability (h^2). To test whether roamers were more likely to sire roamers and territorial breeders more likely to sire territorial breeders, we compared the ratio of sons that became roamers to sons that became territorial breeders between fathers of the two tactics using the Fisher's exact test.

DATA ANALYSIS AND STATISTICS

We used number of pups sired as our fitness estimate. This was standardized as relative fitness by dividing each male's value by the mean for the year. As individual males only breed for one spring breeding season, this was a proxy of relative lifetime reproductive success. For analyses of covariance (ANCOVA), we square-root transformed relative fitness and used single degree of freedom treatment contrasts for tests of significance of effect sizes. For comparisons over all years, we also square-root transformed body mass and centred it at zero. We fit a model with relative fitness as the dependent variable and mass, tactic and year and all interactions as explanatory variables. We used methods of model simplification after Crawley (2007), and within models

we test with the *t* distribution differences between intercepts and slopes using contrasts. Confidence intervals were calculated in the stats package in R. The software packages SAS 9.1.3 and R 2.12.0 (R Development Core Team (2010)) were used. Data are presented as mean ± SD. Correlations were tested using Spearman correlations coefficient r_s.

Results

BODY MASS DIFFERENCES

Males differed in body mass between tactics and years (Table 2, ANOVA, $F_{5,84} = 18·69$, $P < 0·0001$). Territorial breeding males were heavier than roamers ($t_{1,84} = 4·76$, $P < 0·0001$) and philopatrics ($t_{1,84} = 7·49$, $P < 0·0001$). Roamers were heavier than philopatrics ($t_{1,84} = 2·20$, $P < 0·035$). In 2007, in the year of intermediate population density, body mass was significantly higher overall ($t_{2,84} = 3·81$, $P < 0·001$).

In 2005, body mass of territorial males correlated with the size of communal female groups ($r_s = 0·60$, $P = 0·03$, $n = 12$), but not in 2007 ($r_s = -0·05$, $P > 0·9$, $n = 5$). Size of communal female groups ranged from 1 to 8 in 2005 (3·5 ± 2·1 breeding females per group), and from 1 to 4 in 2007 (2·4 ± 1·1 breeding females per group).

COMPARISONS OVER ALL YEARS

Tactic, body mass and year and several of their interactions influenced relative fitness (Table 3; ANCOVA, $F_{8,81} = 18·64$, $P < 0·00001$). Analysis of contrasts within this model showed that the territorial breeding tactic gave higher fitness

Table 2. Body mass (mean ± SD) in grams and sample size (in brackets) of males

Population density	Year	Territorial breeders	Roamers	Philopatrics	Population mean
High	2005	56·1 ± 9·9 (12)	43·5 ± 7·9 (15)	38·8 ± 6·0 (32)	43·5 ± 9·7
Intermediate	2007	58·0 ± 8·6 (5)	54·9 ± 3·6 (8)	(0)	56·1 ± 5·9
Low	2003	(0)	47·2 ± 6·0 (18)	(0)	47·2 ± 6·0

Philopatrics born during the breeding season studied are not included.

Table 3. Parameter estimates from analyses of covariance of mass, tactic and year on fitness after model reduction

Term	Parameter estimate	Lower 95% confidence limit	Upper 95% confidence limit	*t*	*P*
Intercept	0·38	0·12	0·65	2·86	0·005
Mass	0·005	−0·25	0·26	0·037	0·971
Tactic B (vs. R)	1·57	1·11	2·03	6·87	0·00001
Tactic P (vs. R)	−0·33	−0·66	0·002	−1·98	0·051
Tactic P (vs. B)	−1·90	−2·37	−1·43	−8·01	0·000001
Year 2003 (vs. 2005)	0·10	−0·26	0·47	0·57	0·567
Year 2007 (vs. 2005)	−0·17	−0·84	0·51	−0·50	0·622
Year 2007 (vs. 2003)	−0·27	−0·94	0·39	−0·81	0·419
Mass: year 2003 (vs. 2005)	1·18	0·58	1·79	3·87	0·0002
Mass: year 2007 (vs. 2005)	0·70	−0·11	1·52	1·71	0·091
Mass: year 2007 (vs. 2003)	−0·8	−1·43	0·47	−1·00	0·319
Tactic B (vs. R): year 2007 (vs. 2005)	−1·43	−2·18	−0·67	−3·78	0·0003

Table 4. Tactic of father for all offspring for which paternity was determined

Population density	Year	Offspring	Sired by territorial breeding male	Sired by roamer	Sired by philopatric
High	2005	101	90	9	2
Intermediate	2007	98	50	48	Not present
Low	2003	98	Not present	98	Not present

than the roaming tactic and the philopatric tactic. Further, the fitness of breeders compared to roamers differed significantly between 2005 and 2007, indicating that breeders had higher fitness than roamers in 2005, but not in 2007. The effect of body mass on fitness also differed between 2005 and 2003, with mass having a stronger effect on fitness in 2003. Body mass alone, controlling for year and tactic, was not a significant predictor of fitness. There were no significant year effects. There was also no significant three-way interaction between mass, year and tactic (ANOVA, $F_{1,78} = 0.55$, $P > 0.46$), nor a significant interaction between mass and tactic ($F_{2,79} = 0.20$, $P > 0.84$); these terms were dropped from the final model presented here.

MALE FITNESS WITHIN GENERATIONS UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

Under high population density in 2005, every territorial male ($n = 12$) had some reproductive success, while 6 of 15 roamers had reproductive success. Only 2 out of 32 philopatrics present at the start of the breeding season sired offspring (Table 4), while none of the philopatrics born between August and October sired any pups. On average, territorial males sired 6.42 ± 4.32 pups, roamers 0.60 ± 1.06 pups and philopatrics 0.063 ± 0.24 pups. ANCOVA analysis of tactic and body mass and their interaction indicated that there was no significant difference between the slopes of mass against fitness for breeders compared to roamers (Fig. 1d, $t_{2,53} = -0.70$, $P > 0.48$) or philopatrics ($t_{2,55} = 0.83$, $P > 0.41$), or for roamers compared to philopatrics ($t_{2,55} = -0.03$, $P > 0.98$). As this interaction was not significant, it was dropped from the model for further analyses. The remaining model indicated that tactic had a highly significant effect on relative fitness ($F_{2,55} = 44.17$, $P < 0.00001$). Territorial breeding males had significantly higher fitness than roamers ($t_{2,55} = -7.95$, $P < 0.00001$) and philopatrics ($t_{2,55} = -9.26$, $P < 0.00001$). Roamers also had higher fitness than philopatrics ($t_{2,55} = -2.29$, $P < 0.03$). Body mass alone, controlling for tactic, had no effect on fitness ($t_{1,55} = 0.04$, $P > 0.96$).

Under intermediate population density in 2007, territorial breeding males and roamers were similarly successful (Table 4). On average, territorial males sired 9.80 ± 13.02 pups and roamers 6.00 ± 8.84 pups. Every territorial male ($n = 5$) and six of eight roamers had some reproductive success. There was no significant effect of body mass ($t_{1,9} = 1.03$, $P > 0.33$) or tactic ($t_{1,9} = 0.47$, $P > 0.65$) or their interaction ($t_{1,9} = 0.45$, $P > 0.66$) on relative fitness (Fig. 1e, ANCOVA, $F_{3,9} = 0.95$, $P > 0.45$).

While in 2005 10 of 12 territorial breeders (83%) had higher reproductive success than the most successful roamer, in 2007 only one of five territorial breeders (20%) had higher reproductive success than the best roamer. This ratio differed significantly between years ($P = 0.03$, Fisher's exact test), indicating that the difference between territorial breeders and roamers in relative fitness between 2005 and 2007 was not simply because of low statistical power in 2007.

Under low population density in 2003, there was a significant effect of body mass on fitness (Fig 1f, linear regression, $t_{1,16} = 2.96$, $P < 0.01$). On average, males sired 4.56 ± 7.99 offspring with 10 (of 18; 56%) males siring no offspring at all and the most successful male siring 29 offspring with 10 different females during the entire breeding season. Five offspring were sired by 2 (of 22; 9%) young males born in September 2003 in our field site. Both of these males had left their natal group and adopted a roaming tactic. No males born in October or start of November ($n = 24$) sired any offspring, even though theoretically they could have sired offspring born in December.

TACTIC, BODY MASS AND MULTIPLE PATERNITY

The incidence of multiple paternity was high in all years: 39·3% of litters when population density was high, 25·0% of litters under intermediate population density and 54·2% of litters under low population density. Territorial breeding males lost a high percentage of paternity to other males: $39.9 \pm 29.3\%$ (range: 0·0–100·0%) of pups were sired by another male than the territorial male of the group ($n = 17$ territorial males from 2005 and 2007). Heavier males were not more successful in siring offspring with extra-group females ($r_s = 0.18$, $n = 40$ males, $P = 0.27$), indicating that these matings were because of female choice, not male dominance, and that females do not use body mass as a criterion for extra-group mate choice. Furthermore, for 12 females, we could compare body mass between their group male (62.1 ± 11.1 g) and the extra-group fathers of her offspring (52.3 ± 7.1 g). Extra-pair fathers were significantly lighter than group males (paired $t_{11} = 3.409$, $P = 0.006$). Including only the eight cases where the extra-group male was a territorial breeder, there was still a trend (paired $t_7 = 2.168$, $P = 0.067$).

INFLUENCE OF THE SIRE'S TACTIC ON HIS SON'S TACTIC?

For sires that were roamers, the ratio of sons that became roamers to sons that became territorial breeders was 1:13

Table 5. Last tactic shown by a male depending on the tactic of his genetic father

	Tactic son			
Tactic father	Philopatric	Roamer	Territorial breeder	SUM
Roamer	0	1	13	14
Territorial breeder	2	1	7	10
SUM	2	2	20	24

(roamers : breeders). For sires that were territorial breeders, the ratio was 1:7 (roamers : breeders). Roamers and territorial breeders did not differ in producing sons that became territorial breeders ($P > 0.99$, Fisher's exact test; Table 5).

Discussion

Genetic parentage studies have significantly increased our knowledge of natural mating systems, but few have collected data over several years representing different generations living under different ecological conditions to provide deeper insight into its evolution. We show that three alternative male reproductive tactics yield different reproductive success for different generations. We found little evidence for a correlation between reproductive success and body mass (= status) within tactics. Our results challenge traditional definitions of strategies underlying ARTs.

Fitness differences between tactics were seen for the generation living when population density was high and females lived in communal groups. Under these conditions, defending a female group as a territorial breeding male was the best tactic, and larger males defended larger multifemale groups. While we did not measure total fitness of all males, because males might also have sired offspring outside of the study area, extra-group paternity is biased towards territorial breeders under high population density (Schradin, Schneider & Lindholm 2010), further strengthening the conclusion that breeding as a territorial breeder is the most successful tactic. This was in agreement with the definition of conditional strategy by Gross (1996) and is similar to the situation in other species, where roaming males (= wanderers in prairie voles, *Microtus ochrogaster*, Ophir *et al.* 2008) or subordinates (in meerkats, *Suricata suricatta*, Young, Spong & Clutton-Brock 2007) have significantly lower reproductive success than territorial males. As expected, being philopatric is a tactic with low reproductive success. This might explain why philopatrics have very high corticosterone levels (Schradin *et al.* 2009) as predicted for tactics where individuals are stressed because they are making the best of a bad job (Moore, Hews & Knapp 1998).

In contrast, in the generation with low population density, males expressed only one tactic, roaming, and some roamers had very high reproductive success. While under conditions of clumped female distributions males should attempt to defend groups of females, under dispersed conditions males should invest resources in searching for these dispersed females (Emlen & Oring 1977; Orians 1969; Ostfeld 1990). Accordingly, which reproductive tactic male striped mice chose depended on female distribution: when female striped mice formed groups, the largest males became the breeding males of these groups (Schradin *et al.* 2009), defending harems within a relatively small territory (Schradin & Pillay 2005b). In contrast, when females lived solitarily, males preferred to roam and occupied large home ranges, overlapping with the home ranges of several single breeding females, which they only visited for copulation (Schradin, König & Pillay 2010). If females are clumped (favouring interference competition), body mass should correlate with competitive ability and reproductive success, while when females are dispersed (favouring scramble competition), selection should favour traits such as search ability. However, this is in contrast to our present study, where body mass (independent of tactic) was important only in 2003, when males were searching for females, but not in 2005, when males defended female groups.

At intermediate population density, with a female-biased sex ratio and a ratio of single breeding females to communally breeding females of close to unity, fitness of roamers was not statistically different from that of territorial breeders. While sample size and thus the statistical power was low for 2007, we found important differences between 2007 with intermediate and 2005 with high population density: when females were living in communal groups, nearly all breeders had higher fitness than all roamers, while several roamers were better than the average breeder when many females bred solitarily. This interpretation was also supported by our comparison over years: fitness between breeders and roamers differed between 2005 and 2007, indicating that breeders were more successful than roamers when females lived communally, but not or to a much lesser extent when many females lived solitarily. The fact that males sired in total more offspring per male in 2007 than in 2005 can be explained by a change of the sex ratio from male biased in 2005 to female biased in 2007 (Table 1), which might be attributed to more males dispersing in years of lower population density, potentially leading to increased male mortality.

Our study does not demonstrate that it is population density *per se* that determines fitness consequences of male ARTs in striped mice. Fitness of the ARTs could be influenced by the relative frequency of the alternative tactics, which we know is density dependent (Schradin, König & Pillay 2010). Additionally, operant sex ratio, the ratio of solitary to communally breeding females and different ecological variables such as food availability and predation pressure could influence fitness outcomes, and some of these factors might correlate with each other and with population density. The important result of our study is that years differ significantly in fitness consequences of ARTs, and this cannot be explained adequately by existing theory.

When two tactics yield the same reproductive success, they could fit either of the definitions of alternative or mixed strategy (Gross 1996). In alternative strategies, males of alterna-

tive tactics differ genetically and are constrained to one tactic, while in mixed strategies ARTs are not the result of different genotypes, i.e. each male could follow any tactic, and the tactic is chosen based on environmental information (thus only one strategy exists; Gross 1996). It has been shown previously that male striped mice regularly switch tactics and that the same individual male can follow all three tactics during his life (Schradin *et al*. 2009), indicating that tactics are not genetically determined. In the present study, roamers were as likely to sire sons that later became territorial breeders as were territorial breeders. Our data suggest that genotype does not strongly predict which tactic will be chosen; though, genetic variation in the expression of switch-points is not ruled out. Low heritability of two tactics with equal fitness fits the definition of mixed strategies, and to our knowledge, no other empirical example fits the predictions of a mixed strategy better than our results from 2007, the year of intermediate population density.

DECISION RULES: MALE STRIPED MICE FOLLOW A SINGLE STRATEGY

A strategy defines the decision rules determining which tactic an individual chooses (Gross 1996), but these decisions rules are rarely (if ever) formulated. We propose that male striped mice follow the same decision rules in every year, i.e. they have a single strategy that can lead to 1, 2 or 3 different tactics in the population. Our study demonstrates that under most environmental conditions, the fitness consequences represent the outcome of what has been traditionally defined as a conditional strategy (as in most years roamers are smaller than territorial breeders; Schradin *et al*. 2009). However, under specific conditions, tactics might yield identical fitness, which is a characteristic of mixed strategies. Thus, our results indicate that the differentiation between conditional and mixed strategies is not an absolute one, and in many species, environmental conditions might exist under which the normally suboptimal tactic yields equal fitness to the (usually) dominant tactic, and others under which only a single tactic will prevail. We call this a single strategy indicating that all males follow the same decision rules, in contrast to alternative strategies, that consist of two or more sets of decision rules (Gross 1996). Here, we suggest decision rules for a single strategy in male striped mice representing a hypothetical model against which future data are to be tested:

1. Decision: To remain philopatric or to disperse?
- Remain a philopatric male if all females breed in communal groups defended by territorial males and your body mass is below the population mean
- Leave your natal group:
  a. If the ratio of single to communally breeding females is > 1·0 (Table 1).
  b. If at the beginning of the breeding season your body mass is above the mean of the population (Table 2), independent of population density.

2. Decision: To become a roamer or try to become a territorial breeder?
- If all females breed solitarily → become a roaming male.
- If you find a group of communally breeding females that are not defended by a male that is larger than you → become the breeding male of this group.

This set of decision rules emphasizes the important point that being a roamer can be the result of two very different processes: (i) an active choice, because many females breed solitarily and roaming is the best tactic or as good as being a territorial breeder. (ii) Result of low competitive ability, i.e. the male chooses to disperse and would choose to become a territorial breeder, but he cannot, because all communal female groups are defended by larger males. This is similar to the situation in stoplight parrotfish (*Sparisoma viridae*) where males start with the tactic of bachelor and the availability of free territories and their relative body size determines when they can switch to the territorial tactic (Cardwell & Liley 1991). In 2003 and 2007, one alternative for roamers would have been to join a singly breeding female and to become monogamous. Defending a single female could be a strategy to reduce multiple paternities, which were more common in 2003, with 54% of litters having more than one sire. However, because of solitary foraging and the fact that female home ranges are larger when population density is lower (Schradin *et al*. 2010c), mate guarding might not be a successful tactic under these circumstances.

EVOLUTION OF SWITCH-POINTS

One main aim in the study of ARTs is to understand the regulation of switch-points, i.e. at which stage individuals switch tactics (Gross 1996). For switch-points to evolve, individuals must show genetically determined variation in their switch-points (Shuster & Wade 2003; Tomkins & Hazel 2007; Taborsky 2008a). Switch-points are typically illustrated by fitness curves, with the suboptimal tactic showing higher fitness at lower status, while the dominant tactic shows higher fitness at higher status (Fig. 1a). The switch-point is the point where these two lines cross, and individuals are expected to switch tactic when reaching this point (Gross 1996; Tomkins & Hazel 2007; Taborsky 2008a).

In striped mice, tactics depend on body mass, with the heaviest males being territorial breeders, intermediate males being roamers and the smallest males being philopatrics (Schradin *et al*. 2009; this study). According to the switch-point model, we expected a correlation between body mass and reproductive success. However, our comparison over years showed that having a higher body mass alone did not increase fitness. Accordingly, larger territorial breeders were not more successful than small territorial breeders, and larger roamers were not more successful than smaller roamers (except for 2003, when roaming was the only tactic, leading to direct male–male competition). Therefore, we found no

linear relationships between body mass and reproductive success within the different tactics and no switch-points could be determined using this approach.

Body mass influences reproductive success in many species, including those with ARTs (e.g. brook trout *Salvenius fontinalis*, Blanchfield, Ridgway & Wilson 2003; horseshoe crabs *Limulus polyphemuus*, Brockmann & Taborsky 2008; dung flies *Scathophaga stercoraria*, Pitnick *et al.* 2009). In bluegills, body condition (combining body mass and body length) but not body mass influences reproductive success (Neff & Clare 2008). Thus, the question arises whether our negative result is because of the fact that we did not measure the correct variable. We think that body mass is the best measurement because it is important in most species, and in polygynous mammals, larger males are more successful in defending multi-female groups than smaller males (Heske & Ostfeld 1990; Adrian *et al.* 2008). In striped mice, body mass strongly correlates with success in territorial encounters (Schradin 2004) and is highly correlated with male tactics (Schradin *et al.* 2009), and larger males had larger multi-female groups in the year of high population density (this study). While Neff & Clare (2008) did not find a significant effect for body mass on reproductive success in bluegills, they found a trend, and this was to be expected, as their measurement of body condition was a correlate of body mass. In contrast, the main influence of body mass we found was on what tactic was expressed. Thus, we do not believe that any other measurement of body condition would yield a significantly different result. By becoming a territorial male, males can increase reproductive success by defending paternity within their group of communally breeding females. However, this is a categorical event (breeding male yes: high fitness/no breeding male: low fitness), not an event along continuous fitness contours depending on body mass.

As our study relies on a relatively small sample size, we cannot distinguish between the two possibilities that body mass has either no or only a weak influence on male reproductive success within tactics. As theory predicts a clear effect of body mass on fitness, the missing evidence in our study needs explanation in both cases. We suggest that the reason why male reproductive success did not correlate well with body mass within tactics is female choice. While breeding males had the highest reproductive success, 40% of offspring within communal groups were sired by other males, which were often territorial males from neighbouring groups (Schradin, Schneider & Lindholm 2010). This indicates conflict between territorial males and their females, because females often preferred to mate with other males. As striped mice are solitary foragers (Schradin 2006), territorial males cannot continuously defend their females, which do encounter males from other groups during foraging (Schradin 2006). Instead, they defend territories encompassing breeding females (Schradin & Pillay 2004). Our data indicate that females often chose other males as mates in addition to their territorial male and that they did not choose large males for extra-group mating. This could explain the lack of relationship within a tactic between male mass and fitness. The factors that make a male attractive for extra-group fertilizations remain an open question.

Conclusions

Conditional strategies have been described for hundreds of species (Gross 1996) but very few studies have actually measured fitness of individual males following different reproductive tactics (exceptions are Ophir *et al.* 2008; Young, Spong & Clutton-Brock 2007), making the assessment of the status dependency of conditional strategies difficult. In fact, while many studies show a relationship between status and tactic, they typically do not conform to single switch-point predictions (Lee 2005). We find that existing theory is inadequate to describe our empirical data and we encourage theorists to review and adjust theory explaining ARTs where no underlying genetic polymorphism can be demonstrated.

Our study demonstrates three important points: (i) Despite the risk of losing a high percentage of paternity to other males (average of 40%), defending females could still be by far the best tactic. Similar results have been found in prairie voles, where territorial monogamous males lose a high percentage of paternity owing to extra-pair fertilizations, but nevertheless have three times higher reproductive success than roamers (Ophir *et al.* 2008). (ii) The differentiation between conditional and mixed strategies is not always an absolute one and can depend on environmental conditions. Instead, we propose the term 'single strategy' if all individuals follow the same (or very similar) decision rules, independent of the current fitness consequences of ARTs, which would be in contrast to alternative strategies with more than one strategy. 3. Fitness differences between tactics might be rather categorical (e.g. roamer vs. territorial breeder category) than continuous along fitness lines. We expect that many more species follow the pattern of categorical fitness differences.

Acknowledgements

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