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Sexual selection and alternative mating behaviours generate demographic stochasticity in small populations

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Recent theory predicts that environmental variation and small population size facilitate the coexistence of alternative phenotypes despite unequal mean fitness. However, traditional studies of reproductive strategies often assume that the stability of alternative mating behaviours relies on equal male fitness. We present results from field observations and experimental manipulations of thermal resources on territories demonstrating the coexistence of alternative reproductive behaviours with unequal fitness. The side-blotched lizard *Uta stansburiana* exhibits two alternative strategies for territoriality: 'usurp' and 'defend'. Paternity analysis revealed significantly greater mean fitness for 'usurpers' than 'defenders' in our study of natural variation. Moreover, variance in fitness was significantly higher for usurpers on both experimental and natural plots, implying that 'usurp' is a risky strategy with potentially large pay-offs or none at all. We show theoretically that significantly higher variance in usurper fitness can allow for coexistence with defenders despite higher mean fitness of usurpers. This coexistence is facilitated by small population size. Our results have general implications for the evolution of alternative strategies and the maintenance of genetic diversity in small populations.

Keywords: alternative strategies; demographic stochasticity; geometric mean; equal fitness; genetic diversity

1. INTRODUCTION

Behavioural polymorphisms within populations may manifest themselves as individuals with diverse life-history traits or alternative mating behaviours (Rubenstein 1980; Gross 1984; Widemo 1998). One of the primary tests of stability proposed in these studies has been the search for equal fitness among alternative tactics (Ryan *et al.* 1992), since a genotype with higher fitness would be expected to replace a genotype with lower fitness. Demonstrating equality of male fitness is inherently difficult, and has remained controversial in field studies (Austad 1984). Recent theory argues that environmental stochasticity and small population size allow the coexistence of alternative phenotypes with equal geometric mean fitness (e.g. Clark & Yoshimura 1993; Ellner 1996).

When populations are small or strategies are rare, between-generation variance in reproductive success can occur due to demographic stochasticity, and as suggested by life-history models (Gillespie 1974; Clark & Yoshimura 1993), alternative strategies with unequal arithmetic mean fitness may coexist. While these ideas are well accepted in the life-history literature, very few studies have considered their importance to studies of behavioural polymorphism, and in particular, alternative reproductive behaviours.

Male side-blotched lizards, *Uta stansburiana*, exhibit one out of three alternative throat colour morphs (orange, blue and yellow), each with an associated mating strategy and territorial behaviour (Sinervo & Lively 1996; Calsbeek 2001). Blue-throated males ('defenders') tend to settle on territories near their natal site (Sinervo & Calsbeek 2002) and defend resources against competitors. Blue males usually employ a mate-guarding strategy and so maintain relatively small territories containing a single female. By contrast, orange males ('usurpers') are ultra-dominant males that defend large territories containing multiple females. Orange males disperse from their natal site, target the highest quality territories for take-over and attempt to usurp resources held by another resident. This makes usurping a very risky strategy to adopt (Kacelnik & Bateson 1996; McNamara 1996), as leaving a territory in pursuit of a higher quality area may lead to a large pay-off, or none at all. Finally, yellow males are not usually territorial (Sinervo *et al.* 2000), but obtain copulations from females on territories of residents or usurpers by using female mimicry.

The two territorial strategies, 'usurp' and 'defend', are similar in that usurpers must also defend sequestered resources; however, we distinguish the two strategies as discrete alternative tactics based on different trade-offs associated with each strategy. For example, defenders may lose territory to usurpers, but by sequestering more territory, usurpers may be susceptible to infiltration by sneaker-male strategies (Sinervo & Lively 1996). Here we are interested in the role of demographic stochasticity in the maintenance of the two territorial strategies, and sneaky strategies of yellow males are treated elsewhere (Zamudio & Sinervo 2000). Because yellow males are not

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157

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territorial, their fitness effect on the two territorial strategies occurs by subterfuge.

The goal of our study was to demonstrate the potential importance of demographic stochasticity in maintaining genetically based alternative strategies. Our experimental approach involved manipulations of territory quality that heightened the degree of sexual conflict normally present in this system, through cascading effects on the distribution of females (Calsbeek 2001). Rock habitat provides a valuable resource to both male and female side-blotched lizards. For lizards, as for all ectotherms, growth rate and adult body size depend on an individual's ability to thermoregulate (Adolph & Porter 1993; Sinervo & Adolph 1994). Even in areas where food is abundant, if thermal resources are limiting, metabolism and therefore growth is constrained by the environment (Sinervo & Adolph 1989). High-quality territories in this population are characterized by both hot and cool sites, since behaviourally thermoregulating animals must shuttle between various temperature regimes to maintain their preferred body temperature (Huey 1982; Adolph 1990). High-quality territories (hereafter referring to richness of thermal resources) should also provide retreat sites from predators and ideal nest-sites for females to lay their eggs. We can easily manipulate territory quality by altering rock abundance on territories (Calsbeek 2001). Males that are able to maintain their territories in the face of our experimental manipulations should experience enhanced reproductive success through their increased access to females.

Although the role of demographic stochasticity has been explored in life-history studies, we extend the theory to alternative reproductive behaviours and present, to our knowledge, its first analytical application to experimental data collected in the wild. Our empirical evidence shows that alternative strategies for territoriality coexist despite large differences in arithmetic mean fitness. We also present theory suggesting that the conditions for coexistence may depend on the influence of intergenerational variation in reproductive success driven by intra-sexual conflict.

2. METHODS

(a) *Field methods*

The study took place on three replicate sandstone rock outcroppings adjacent to Billy Wright Road in Merced County, California, USA, near Los Baños Grandes. Early each spring we captured all *U. stansburiana* on the outcroppings, recorded sex, snout–vent length (mm) and mass (g), and assigned a unique toe clip and dorsal paint mark to each animal. Paint marks were used to facilitate visual identification in the field, while toe clips provided a form of permanent identification and a tissue sample to be used in molecular analyses of paternity. All male throat colours were scored at the onset of the breeding season as either blue, orange or yellow by recording the colour displayed on the underside of the male's throat (Sinervo & Lively 1996). Male territory strategy (throat colour) is genetically determined and is highly heritable ($h^2 = 0.86$) (Zamudio & Sinervo 2000).

Territory distributions were measured (Sinervo & Lively 1996) for a total of 249 males in the wild from 1992 to 1996 ($n = 72$ orange and 177 blue). Home ranges were mapped from daily visual censuses (Sinervo & Lively 1996) (means of 8.1, 5.6, 9.6, 15.5 and 13.8 sightings per male, based on $n = 1846$, 1791,

3466, 1664 and 1078 total sightings from 1992 to 1996, respectively). Territories were defined as areas guarded exclusively by one male. A male was considered to have usurped a territory when he appeared on a territory previously defended by another male, who then appeared elsewhere on the rock outcropping. Males filling vacancies left by males that died were not considered to be usurpers.

In 1998 and 1999 we captured and measured territories for 34 males prior to and after manipulating territory quality. We also recorded territory usurpations exactly as had been done between 1992 and 1996. Home ranges were mapped (Sinervo & Lively 1996) from daily visual censuses (means of 7.7 and 6.9 sightings per male based on $n = 307$ and 367 total sightings in 1998 and 1999, respectively). After initially mapping territories, we removed the rock habitat from territories of half the males and deposited it on the territories of neighbouring males. We resumed territory mapping for all males and females on the outcrop, beginning 4 days after our manipulations. This time-frame has proved sufficient to allow all interactions between neighbours to stabilize (DeNardo & Sinervo 1994). We tracked changes in the distribution of all males and females among territories on the study plots, and also monitored all surrounding rock outcroppings out to a distance of 1 km. This would have allowed us to record any dispersal events that may have occurred as a result of the territory manipulations. None were recorded.

(b) *Paternity analysis*

We measured reproductive success as the number of offspring sired per male. Because side-blotched lizards are 'annuals', dying after a single season of reproduction, paternity analysis allowed us to estimate life-time reproductive success for individual males. Survival differences among males would not, therefore, contribute additional variance to estimates of male fitness. Moreover, hatchling survival is not morph dependent (Zamudio & Sinervo 2000), thus paternity analysis provides an excellent estimate of male reproductive success. Paternity was estimated using nine microsatellite loci cloned from a single *U. stansburiana* from the Los Baños Grandes population in Merced County. Loci were cloned from genomic DNA by standard cloning methods (Zamudio & Sinervo 2000). Genomic DNA was extracted from toes by overnight incubation at 55 °C in 500 μl of 5% Chelex (Biourad, Hercules, CA, USA) and 2 μl of proteinase K solution (at 20 mg ml^{-1}) followed by centrifugation and 1 : 10 dilution of the extract. Loci were amplified from the genomic template via PCR, and length polymorphism among individuals was assessed with fluorescent labelling of the forward primers on an automated DNA sequencer (ABI 377, Applied Biosystems, Foster City, CA, USA).

Eggs were collected from females on clutches 1–3 and were incubated under standard conditions (Sinervo & Adolph 1989, 1994). We genotyped tissue collected from all animals on natural plots in 1992 ($n = 458$, 96 and 125 for progeny, dams and sires, respectively), 1996 ($n = 160$, 68 and 56) and on experimental plots in 1999 ($n = 69$, 19 and 53). Paternity was assigned with maximum likelihood, which incorporated exclusionary criteria (Goodnight *et al.* 1996). A male was accepted as a hatchling's sire if the likelihood of paternity was significantly different from that expected for unrelated males ($p < 0.05$). Paternity was assigned to 71% of progeny for 1992, 75% of progeny for 1996 and 71% of progeny for 1999 (i.e. we assigned paternity to a total of 494 progeny). Progeny to which sires could not be accurately assigned were not included in our measures of reproductive success. While paternity analysis provides an estimate of

male reproductive success, the few progeny not assigned to sires each year probably represent a random subset of the population of juvenile lizards. Thus our fitness estimates for the two territorial morphs are not likely to have been biased by a 75% success rate of paternity assignment. We would only have expected a biased estimate of paternity if microsatellite markers were somehow distributed non-randomly between morphs. Moreover, all males, including those males with zero paternity, were included in our analyses.

To estimate paternity we used detailed territory maps available for each year (Sinervo & Lively 1996). Plots formed isolated rock outcrops separated by unsuitable habitat. We searched for putative sires within a dam's neighbourhood (e.g. plot) and assigned as the sire the male with the highest significant likelihood. In addition, we analysed paternity by searching all males in the dam's adjacent neighbourhood (adjacent plots). Males from this larger area were assigned as the sire if their likelihood values were higher than those for males in the dam's immediate neighbourhood. Restricting the paternity search to neighbouring plots is conservative and biologically relevant. Few males (less than 5% of sightings) move between plots and no male has been seen moving beyond adjacent plots (based on $n = 2328$ map locations).

We tested the prediction that the variance in fitness of usurpers was greater than that of defenders by randomizing reproductive success across identities of males in our experimental populations. The randomization test entailed four random draws without replacement from a pool of 34 usurpers and defenders. Throat-colour (i.e. strategy) frequencies in the pool were identical to frequencies observed in nature. We calculated the probability that variance in reproductive success would be as great as that observed in the usurper class (1000 randomizations).

(c) *The model*

We used a continuous version of a classic single locus haploid game theoretical model to explore the general conditions required for coexistence of the alternative male strategies, 'usurp' and 'defend'. We calculate the expected mean and variance in individual reproductive success of the 'usurp' and 'defend' strategies, and show how intra-sexual competition can facilitate the stable coexistence of alternative strategies with unequal mean fitness.

Usurpers target high-quality territories but if unsuccessful they gain nothing. By contrast, defenders maintain lower-quality territories but experience more consistent fitness gains. Let p represent a usurper's probability of successfully usurping and keeping a high-quality territory. Let τ represent the threshold value of territory targeted by usurpers and $F(x)$ the distribution of reproductive success on territories (figure 1). We assume that the frequency of usurpers determines the threshold τ as usurpers 'fill up' the high-quality territories. It is further assumed that usurpers attempt only one takeover. The threshold will depend on usurper frequency f in the population such that

$$f = \int_{\tau}^{\infty} F(x)\,\mathrm{d}x. \qquad (2.1)$$

Usurpers gain reproductive success from the distribution above τ with probability p, or gain nothing from their efforts with probability $(1 - p)$. The mean reproductive success of individual usurpers (U) will be
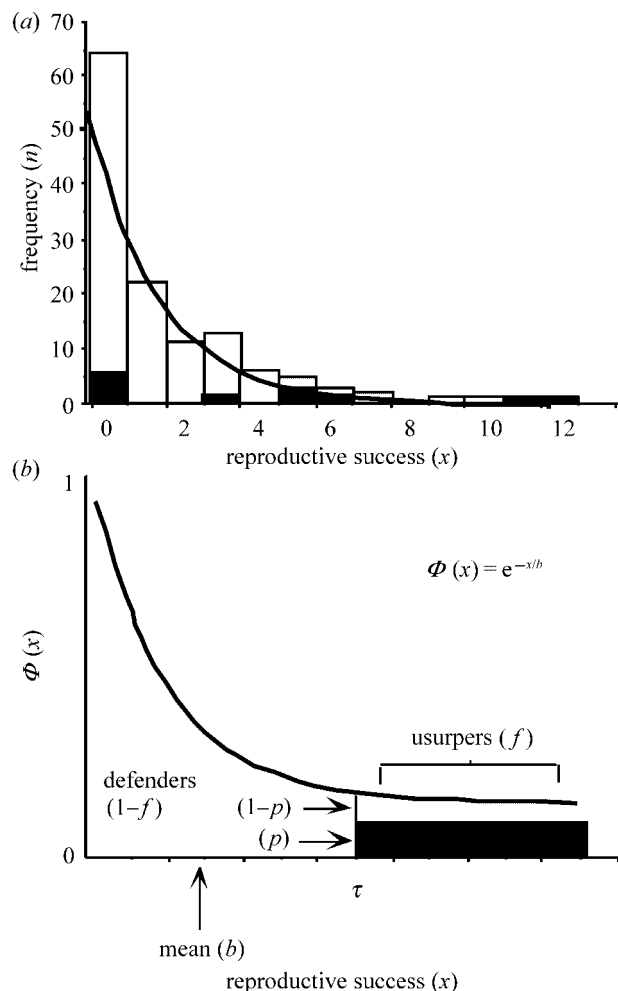

Figure 1. (*a*) Win–lose dynamics generate among-year variation in fitness. This shows the observed distribution of reproductive success on natural plots in 1992 (white bar). The distribution of fitness on outcrops approximates an exponential distribution (heavy line, $r^2 = 0.94$, $p = 0.001$) with mean reproductive success equal to 1.87 offspring. The observed distribution of fitness for usurpers on all plots is given in black bars. (*b*) Usurpers target high-quality territories and experience reproductive success above a threshold value τ determined by the frequency of usurpers f, but only a fraction (p) are successful sires. Having targeted territories for usurpation, reproductive pay-offs are either very high or zero for a given probability of success. This win–lose dynamic generates high variance in reproductive success among usurpers. By contrast, defender males experience fitness across the rest of the distribution. While defenders experience lower mean reproductive success than usurpers, the variance in defender success is also low. We propose that this difference in variance maintains two alternative strategies despite unequal mean fitness and can maintain genetic diversity in mating behaviour in small populations.

$$U = \frac{p}{f} \int_{x = \tau}^{\infty} xF(x)\,\mathrm{d}x, \qquad (2.2)$$

and the variance in individual reproductive success is given by

$$\sigma_U^2 = \frac{p}{f}\left(\int_{\tau}^{\infty} F(x)(x - U)^2\,\mathrm{d}x\right) + \frac{1 - p}{f}(U)^2. \qquad (2.3)$$
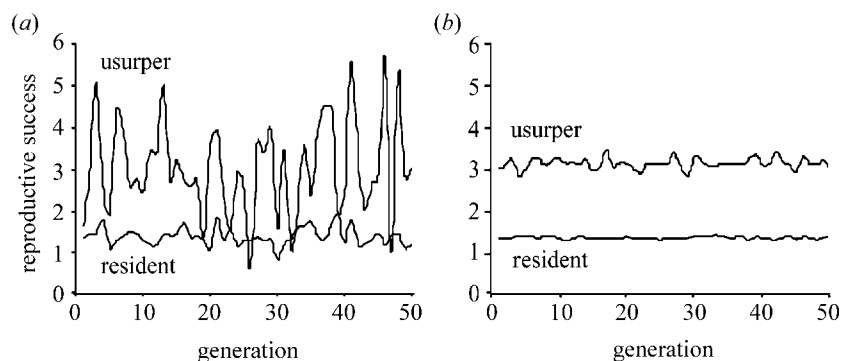
Figure 2. (*a*) We simulated between-year variance in success of both usurpers and residents based on paternity data (figure 1*a*), the model of wins and losses (figure 1*b*), the observed distribution of reproductive success for territories targeted by usurpers (e.g. $\tau = 5$), and probability of success for usurpers on natural and experimental plots (e.g. five usurpers with wins greater than τ and six with losses less than τ). We simulated success of 11 usurpers and 130 residents over 1000 runs (50 generations are shown). The simulated between-year variance in mean fitness for orange usurpers (3.81) was much larger than between-year variance for resident males (1.02). (*b*) Increasing population size of each class 10-fold, while holding relative frequency of strategies constant decreases the absolute but not relative difference between the two strategies in among-year variance in mean fitness.

Similarly, the expected mean fitness of defenders will be the mean of the distribution below τ, which is

$$D = \frac{1}{1-f} \int_{x=0}^{\tau} xF(x)\mathrm{d}x. \qquad (2.4)$$

Finally, the individual variation in reproductive success of defenders will be equal to the variance in the distribution below τ, or

$$\sigma_D^2 = \frac{1}{1-f} \int_{x=0}^{\tau} F(x)(x-D)^2\mathrm{d}x. \qquad (2.5)$$

Usurpers target territories with the highest potential reproductive benefits but only a fraction of those who usurp are successful sires. Successful usurpers sire many progeny (as shown in figure 1*b*), while the rest sire none at all. Variance in usurper mating success is high (figure 2) because usurping is such a risky strategy (Kacelnik & Bateson 1996; McNamara 1996).

Between-generation variance in usurper fitness will depend on individual variance in mating success and the total number of usurpers in the population. In small populations, when variance in usurper success is large, fitness is best represented by the geometric mean. As population size and the number of usurpers increase, variance in usurper fitness will decrease. In very large populations the variance in expected fitness approaches zero, and equality of arithmetic mean fitness would be necessary for the stable coexistence of the two strategies. However when demographic stochasticity generates variance in between-generation fitness for usurpers and defenders, both strategies can coexist where their geometric mean fitnesses are equal.

To explore the effects of demographic stochasticity on the conditions for coexistence of strategies with unequal fitness, we performed a series of simulations by evaluating equations (2.1)–(2.5), and finding the conditions necessary for coexistence of the two strategies with and without demographic stochasticity. In order to evaluate the equations, we assumed that reproductive success $F(x)$ was distributed exponentially. An exponential dis-

Table 1. Contingency table analysis and summary of territory takeovers versus defenders, observations made from 1992 to 1996 as a function of throat colour.

(Orange males were significantly more likely than blues to be territory usurpers because of the high resource usurping potential of orange-throated males ($\chi^2 = 13.02$, d.f. = 1, $p = 0.003$, see also results from randomization tests in § 3a). All defenders that lost their territories were blue-throated males.)

	blue	orange
usurpers	3	9
defenders	174	63

tribution closely approximates the observed distribution of reproductive success (figure 1*a*). We then simulated the ability of each strategy to invade a population that was nearly fixed for the alternative strategy. The simulations explored the following parameter space: p ranging from 0 to 1 (in increments of 0.1) and n ranging from 10 to 12 000 (in increments of 10). Finally, we compared the importance of demographic stochasticity to each strategy's ability to invade the alternative strategy, by performing our simulations with and without stochasticity in parameter p.

3. RESULTS

(a) *Experimental manipulations of territory quality*

High-quality territories enhance progeny fitness. In 1999 a new cohort of hatchlings was allowed to recruit to territories that were manipulated in 1998. Hatchlings that recruited to territories containing experimental rock additions were significantly larger (mean body size = 8.01 g) than hatchlings that did not secure high-quality territories (6.92 g) (ANOVA$_{1,23}$ $F = 8.46$, $p < 0.008$). We also saw a significant redistribution of females on to sites with rock additions (37 females moved towards rock additions and 14 away; $\chi^2 = 10.21$, d.f. = 1, $p < 0.001$). Thus, females significantly preferred rock additions, and progeny also grow to be larger on improved territories.

Table 2. Arithmetic mean reproductive success (with standard errors) for defender males and orange usurpers on natural plots and experimental plots.
(On natural plots, orange-throated usurpers sired significantly more offspring than did defenders (randomization test, $p = 0.011$). On experimental plots, the difference in reproductive success (RS) between orange usurpers and defender males was not significant ($p = 0.3$), even though there was more than a threefold difference in reproductive success. It is noteworthy that the variance in reproductive success was significantly different between usurpers and defenders on both natural plots (randomization test, $p = 0.008$) and experimental plots ($p = 0.001$).)

plot and type of male	n	mean RS	s.e.
natural plots			
all defenders	121	1.47	0.20
orange usurpers	6	4.33	1.84
experimental plots			
all defenders	30	0.80	0.22
orange usurpers	4	2.75	2.75

Males should therefore attempt to control rock piles to acquire more copulations from females.

Female movements towards rock additions were followed by four incidents in which males who lost rocks took over the territory of a rival that gained rocks. In three out of the four territory takeovers, orange males usurped territories from neighbouring blue males. The fourth case was more complicated in that territory shifts involved a three-way interaction among males. A neighbouring orange male on a reduced-quality territory usurped the territory of an orange neighbour that had received an improved territory. The evicted orange male then usurped a high-quality territory from the resident blue male, who subsequently disappeared from the outcropping. None of the usurpations on experimental plots were by blue-throated males.

We tested the prediction that territorial usurpers were most likely to be orange-throated males by randomizing territory usurpation results across throat identities of males in our experimental populations. Our randomization test entailed four random draws without replacement from a pool of the 34 throat scores observed in nature. We calculated the probability that all four observed territory usurpations would be by orange-throated males (1000 randomizations, $p < 0.01$). This measure may be affected by the single case of non-independence in the three-way interaction. However, even when we exclude the one individual and consider only dyadic encounters, our result is still significant (1000 randomizations, $p < 0.04$).

Territory usurpation on natural plots occurred at a low frequency (12 out of 249 males) and as was the case on experimental plots, usurpers on natural plots were significantly more likely to be orange than blue males (table 1, $\chi^2 = 13.02$, d.f. $= 1$, $p < 0.001$). All evicted males on natural plots had blue throats.

DNA microsatellite paternity analysis revealed significantly higher arithmetic mean reproductive success for orange-throated usurpers compared to defenders on our natural plots ($p = 0.01$, table 2). The same pattern showed up on experimental plots, but the nearly threefold greater fitness of usurpers over defenders was not significant owing to small sample size and extremely high variance in the usurper strategy. When we pooled fitness data from both plots, the consensus combined p-value was still significant ($p < 0.01$). Moreover, the variance in fitness of usurpers was significantly greater than variance in fitness of defenders on both natural ($p = 0.008$) and experimental plots ($p = 0.001$). The three blue males that did usurp territories on natural plots were not successful sires (mean reproductive success of 0.67, s.e. $= 0.67$, c.f. table 2). The results indicate that the usurper strategy of orange males has a high but extremely variable pay-off. Previous work has demonstrated that the alternative mating strategies present in this system cycle in a evolutionarily stable state (Sinervo & Lively 1996). Classical game theory (Maynard Smith 1974) considered the importance of frequency dependence, but studies that simplify these ideas to equal fitness cannot explain stability in this population since genetically determined alternatives with unequal fitness are predicted to go to fixation. Therefore, we present results from our model outlining how dynamics common to many mating systems may influence the stable coexistence of alternative behaviours with unequal fitness.

(b) *Model implications based on field data*

The nature of a 'winner takes all' mating strategy inherently generates high variability in mating success among individuals within a given year. In small populations, this individual variation in fitness can generate intergenerational variation in the fitness of a strategy. Because of the high variance in usurper mating success, inter-annual variation in mean mating success of the 'usurp' strategy will also be high in small populations. By contrast, defenders have considerably less variation in mating success both within and between years. We measured the fitness of orange males and blue males (DNA paternity) (Goodnight *et al.* 1996) on seven independent outcrops (e.g. separate populations) in two years and computed the difference in fitness of male strategies on each outcrop between years. The between-year difference within populations for mean fitness of orange males and blue males estimates between-year variance in fitness. The mean between-year variance was significantly higher for orange males ($\sigma^2 = 7.880$) compared to blue males ($\sigma^2 = 0.480$) ($\chi^2 = 6.61$, d.f. $= 1$, Bartlett's test of homogeneity of variance, $p = 0.01$).

In large populations, equality of arithmetic mean fitness of usurpers and defenders would be necessary for stable coexistence in our model. However, in small populations when demographic stochasticity generates variance in between-generation fitness for usurpers and defenders,
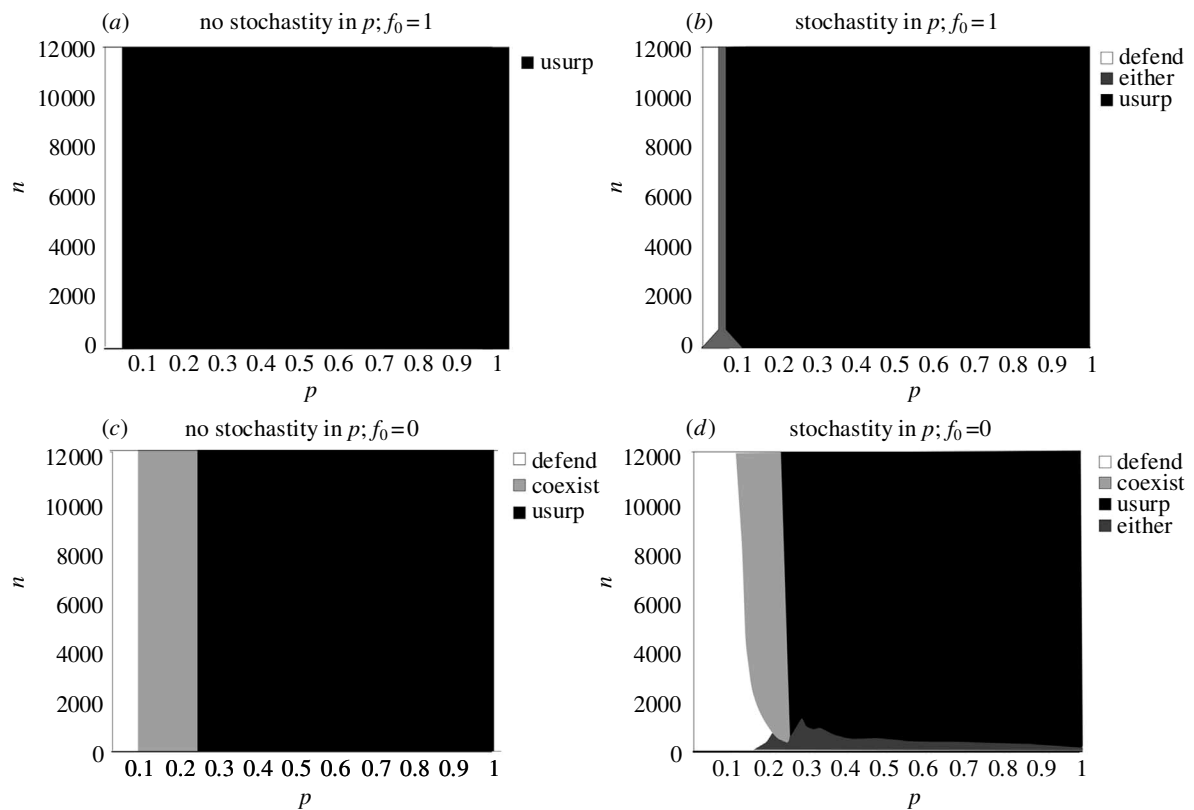
Figure 3. In small populations, demographic stochasticity and win–lose dynamics generate high variance in reproductive pay-offs among usurpers that alter the conditions for coexistence with the less successful but less variable 'defend' strategy. Assuming no demographic stochasticity, a population fixed for usurpers (i.e. $f_0 = 1$) can not be invaded (*a*). However, demographic stochasticity may facilitate invasion by defenders. Either of the two strategies may then go to fixation depending on drift (*b*). In the absence of demographic stochasticity, a population of all defenders (i.e. $f_0 = 0$) may be invaded by usurpers given a sufficiently high probability of usurper success ($p > 0.24$) (*c*). Demographic stochasticity again alters the conditions for coexistence, and, as in the case described by (*b*), either strategy may go to fixation depending on drift (*d*).

both strategies can coexist where geometric mean fitnesses are equal, because the large variance in usurper fitness leads to a smaller geometric mean. If we consider equality of geometric mean fitness to be important, then in small populations the two alternative strategies will be differentially affected by their respective variance in fitness. In large populations, the effects of demographic stochasticity become less important as the variance in usurper success approaches zero.

Our model simulations demonstrate that the invadability and coexistence of the two alternative strategies depend on the effects of demographic stochasticity as well as the initial frequencies of the two strategies (figure 3). Starting with a population of all usurpers (i.e. $f_0 = 1$) and no stochasticity in the parameter p, defenders are unable to invade. However, adding a stochastic component to usurper success leads to parameter values where defenders may invade and overcome usurpers, or where either strategy may outcompete the other depending on drift. Starting with a population of all defenders (i.e. $f_0 = 0$) and no stochasticity in the parameter p, usurpers may invade and overcome defenders given a sufficiently high probability of success (e.g. $p > 0.24$). In our simulations, values of p between 0.1 and 0.24 were suitable for stable coexistence of the two strategies. Finally, adding a stochastic component to usurper success and starting with a population of all defenders alters the conditions for coexistence, and adds a new parameter space where, as in the second case

described above, either strategy may go to fixation depending on drift (figure 3).

In general, stable coexistence of the two alternatives is possible even in the face of unequal fitness. Given a population composed of both alternative strategies, variance in mating success due to demographic stochasticity will alter the conditions that lead to stable coexistence. In small populations, drift may play a critical role in that for some parameter values, a single strategy may fix where the two strategies would otherwise coexist.

4. DISCUSSION

Both our theoretical and empirical results suggest that small population size can maintain genetic diversity in alternative reproductive strategies. This maintenance is affected by demographic stochasticity within the context of limited gene flow among meta-populations. The nature of lizard territories in our study provides particularly strong support for our argument, since lizards set up territories in small neighbourhoods of a few males (for example, seven males), effectively generating a large number of very small populations with limited gene flow.

Our theoretical results suggest that demographic stochasticity can have a major effect on the maintenance of alternative strategies. In many systems, a 'winner take all' dynamic arising due to sexual selection leads to high variance in male reproductive success, which in small popu-

lations will alter the conditions necessary for stable coexistence of alternatives. Moreover, we argue that dynamics common to many mating systems lead to variation in mating success that can alter patterns of genetic diversity within small populations. It is important to note that the role of population size in our model is paramount. Small populations may be at an increased risk of extinction (Ginsberg *et al.* 1995), however, both our theoretical and empirical results suggest that a very large population with many small genetically isolated subdivisions may sustain genetic diversity as a result of demographic stochasticity.

This same process can occur with no restrictions on population size when environmental variation differentially affects alternative strategies. For example, if one strategy is more affected by stochastic changes in environmental conditions, then we expect the fitness of a strategy to vary between years. Recent theory concerning environmental stochasticity suggests that inter-generational variation in fitness can dramatically alter the maintenance of phenotypes (Yoshimura & Clark 1993). Inter-generational variation may also affect the conditions under which alternative strategies coexist in a population.

We have shown that inter-generational variance in reproductive success can alter the conditions for coexistence of two strategies with unequal arithmetic mean fitness. While we acknowledge that small populations are not free from the effects of drift, negative frequency dependence will decrease the probability that any morph will be lost due to drift. Furthermore, the existence of multiple small populations would allow for re-invasion by any morph lost from that neighbourhood due to drift. This process is illustrated in figure 3*b*,*d*, where either strategy may be lost and/or reintroduced by drift-like processes between neighbourhoods.

Inherent risks in adopting the 'usurp' strategy result in high variance in mating success. This variance affects the coexistence of the two genetically based alternative strategies. Coexistence is possible however, even in the face of a large difference in arithmetic mean fitness, albeit similar geometric mean fitness. Empirically, equality of mean geometric fitness will be difficult to demonstrate. Thus, the study of high-variance alternative reproductive behaviours like usurper strategies should focus on mechanisms maintaining coexistence such as frequency dependence (Sinervo & Lively 1996; Zamudio & Sinervo 2000) rather than demonstrating equal male fitness (Rubenstein 1980; Gross 1984).

Finally, recent work has emphasized the importance of understanding behaviour in studies of population dynamics (Smith *et al.* 2000). We suggest that understanding the behaviour and underlying genetics of mating systems is essential for predicting the maintenance of genetic diversity in small populations (Westemeier *et al.* 1998). In particular, our results may lend new insight towards understanding the use of a single large population versus many small genetically isolated populations when attempting to preserve genetic diversity in endangered species (Simberloff & Abele 1975), and particularly genetic diversity in behaviour.

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