Decreased sexual signalling reveals reduced viability in small populations of the drumming wolf spider *Hygrolycosa rubrofasciata*

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One of the important goals in conservation biology is to determine reliable indicators of population viability. Sexual traits have been suggested to indicate population extinction risk, because they may be related to viability through condition dependence. Moreover, condition-dependent sexual traits may be more sensitive indicators of population viability than early life-history traits, because deleterious fitness effects of inbreeding tend to be expressed mainly at the end of the species' life history. However, empirical evidence of the significance of sexual behaviour for population viability is missing. In this study, we examined two male sexual traits and survival in 39 different-sized and isolated natural populations of the wolf spider, *Hygrolycosa rubrofasciata*. We also used several traits to estimate female reproductive success in 25 populations of *H. rubrofasciata*. According to previous studies, *H. rubrofasciata* males have a costly and condition-dependent acoustic signal, courtship drumming, which is the target of female choice. Males with a high drumming rate have considerably higher viability than males with a low drumming rate, and females that mate with the more actively drumming males gain genetic benefits in terms of increased offspring viability. Our results show that males in small populations had both lower survival and lower drumming rate than males in larger populations. However, we did not find any evidence for a decline in important early life-history traits (offspring number, hatching success or offspring body mass) or female body mass in small populations. Our results have two important messages for conservation biology. First, they show that sexual traits can be used as sensitive indicators of population viability. Second, the indirect benefits of female choice in terms of good genes might partially compensate for the reduction of viability in declining populations. Also, our results support the view that deleterious effects of small population size are expressed at the end of the species' life history.

Keywords: wildlife conservation; sexual selection; population status; reproduction

1. INTRODUCTION

Identifying behavioural traits that reflect and affect population viability has been suggested to provide a paradigm for integrating behavioural ecology into conservation biology (Curio 1996; Clemmons & Buchholtz 1997; Strier 1997; Caro 1998; Sutherland 1998; Anthony & Blumstein 2000). Behaviour can decrease effective population sizes through at least three different mechanisms: (i) by reducing population size (e.g. emigration or infanticide); (ii) by reducing population growth rate (e.g. reproductive suppression of adults); and/or (iii) by increasing reproductive skew (e.g. active mate choice, dominance interactions or sex-dependent dispersal) (Anthony & Blumstein 2000). Also, small population size can have a negative impact on the species' behaviour. For example, a small population size can cause social dysfunctions (Allee 1931; see also Sutherland 1998). Thus, behaviour interacts with population size in many different ways that decrease effective population sizes, thereby increasing the deleterious effects of small population size on population viability.

Sexual selection can have many contradictory effects on population viability (Kokko & Brooks 2003). Intense sexual selection may increase the risk of population extinction by increasing the costs of sexual traits (Tanaka

1996; Gosling & Sutherland 2000; Houle & Kondrashov 2002). For example, introduction probability to islands has been shown to be considerably smaller in dichromatic than in monochromatic bird species (McLain *et al.* 1995; Sorci *et al.* 1998). Plumage dichromatism is supposed to have evolved under sexual-selection pressures, which probably make dichromatic species more vulnerable to extinction than monochromatic species. Recently, Doherty *et al.* (2003) analysed the dynamics of natural bird communities on a continental scale and showed that sexual selection increases the risk of local extinction. Sexual selection can also increase the probability of population extinction through effects on population structure. For example, sexual selection can generate mating skew, which may reduce effective population sizes and increase the loss of genetic diversity in small and isolated populations (Anthony & Blumstein 2000; Gosling & Sutherland 2000; see also Westemeier *et al.* 1998; Höglund *et al.* 2002). However, sexual selection can also have positive effects on viability in small populations. First, a theoretical model predicts that, in small populations, sexual selection may act to reduce the fixation probability of deleterious new mutations and increase the probability of fixing new beneficial mutations (Whitlock 2000). Second, females may avoid the costs of inbreeding by multiple mating (Tregenza & Wedell 2002) or by avoiding mating with inbred males (e.g. Reusch *et al.* 2001).

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An increase in sexual activity has been demonstrated to decrease male viability through physiological and/or direct costs. Physiological costs are manifested as increased energy consumption (e.g. Taigen & Wells 1985; Kotiaho *et al.* 1998*a*), whereas direct costs may take the form of increased predation risk or parasitism (e.g. Cade 1975; Ryan 1985; Kotiaho *et al.* 1998*b*). Costly male sexual traits are good candidates for indicators of population viability, because they may be linked to viability through condition dependence (Gosling & Sutherland 2000; see also Andersson 1986, 1994; Johnstone 1995). This is because males in a good condition may be better able to bear the viability costs of developing and maintaining sexual traits than males in a poor condition. Therefore, condition-dependent sexual traits may sensitively signal viability or 'good genes' to choosy females, and females may choose males with large sexual traits as mating partners (review in Møller & Alatalo 1999; see also Kotiaho 2001). However, condition-dependent sexual traits may be sensitive indicators of demographic, environmental and genetic fluctuations for scientists. However, despite the need to determine reliable indicators of population viability in the face of increasing habitat loss, sexual traits have so far, to our knowledge, not been studied in this context.

Inbreeding depression is the reduction in the mean value of a phenotypic trait (Charlesworth & Charlesworth 1987). It is most likely to occur in small and isolated populations where coalescence times (i.e. the time to the most recent common ancestor) are much shorter than in larger and less isolated populations. There are several theoretical models suggesting that the timing and magnitude of inbreeding depression may vary depending on the stage of the species life history. Inbreeding depression expressed in early life-history traits may be caused by a few lethal alleles (Lande & Schemske 1985; Charlesworth & Charlesworth 1990). However, these alleles are effectively purged from the population. Inbreeding depression expressed in later life-history traits may largely be caused by mildly deleterious recessive alleles (Charlesworth *et al.* 1990, 1991). These alleles are expected to survive longer in the population's gene pool. Therefore, inbreeding depression may be manifest in later stages of the life history, as mildly deleterious alleles are not as effectively purged. Despite these important theoretical consequences of inbreeding in different life-history stages, there are only a few animal studies that have tested these predictions in wild populations (Keller & Waller 2002; but see Coulson *et al.* 1998, 1999; Slate *et al.* 2000).

The wolf spider, *Hygrolycosa rubrofasciata* (Ohlert 1865), (Araneae: Lycosidae) has an acoustic signal, drumming, which is used for sexual communication. During the mating season (April until June), males of *H. rubrofasciata* produce drumming signals by hitting their abdomens on dry leaves or some other suitable substratum to court females (Kronestedt 1996). One courtship drumming consists of *ca.* 30–40 separate pulses, lasts *ca.* 1 s (Rivero *et al.* 2000) and is audible to the human ear up to a distance of several metres. In *H. rubrofasciata*, male courtship drumming rate has been demonstrated to be an honest viability indicator for choosy females (Kotiaho *et al.* 1996, 1999; Mappes *et al.* 1996; review in Ahtiainen *et al.* 2001). Females prefer males with a high drumming rate as mating partners (Kotiaho *et al.* 1996; Parri *et al.* 1997). In *H.*

rubrofasciata, males are polygynous, whereas females seem to copulate only once (J. J. Ahtiainen, R. V. Alatalo, J. Mappes and L. Vertainen personal observation). Male drumming incurs both physiological (Mappes *et al.* 1996; Kotiaho *et al.* 1998*a*) and predation costs (Kotiaho *et al.* 1998*b*), which eventually cause the death of males at the end of the mating season (J. J. Ahtiainen, R. V. Alatalo, J. Mappes and L. Vertainen unpublished data). Survival costs of male drumming are condition dependent, so that males in poor condition have both lower viability and lower drumming rate than males in good condition (Mappes *et al.* 1996; Kotiaho 2000). By choosing males with the highest drumming rates, females benefit through better offspring survival (Alatalo *et al.* 1998). Also, male mobility is positively associated with male mating success (Kotiaho *et al.* 1998*b*). In *H. rubrofasciata*, male body mass does not seem to be intersexually selected and is not correlated with male mating success (Kotiaho *et al.* 1996; Mappes *et al.* 1996). Consistent with other spider taxa, *H. rubrofasciata* females with a high body mass lay larger clutches than females with a low body mass (Vertainen *et al.* 2000; see also Marshall & Gittleman 1994; Simpson 1995). However, offspring body mass seems to be independent of clutch size.

In this study, we examine the effect of population size on male drumming rate, mobility and survival in 39 natural populations of *H. rubrofasciata*. No field studies on natural populations, to our knowledge, have been conducted to test the significance of sexual traits in revealing the decline of viability in small populations. We also examine the effect of population size on five estimates of female reproductive success (the numbers of live and undeveloped dead offspring at hatching, hatching success and offspring and female body mass) in 25 natural populations of *H. rubrofasciata*. *Hygrolycosa rubrofasciata* is a ground-dwelling non-social wolf spider, which can be found in patchily located populations widely distributed over northern Europe. *Hygrolycosa rubrofasciata* inhabits two kinds of habitat: abandoned fields and other meadow habitats, and half-open bogs with deciduous trees (*Betula* spp., *Salix* spp.), moss (*Sphagnum* spp.) and grasses (*Carex* spp., *Eriophorum vaginatum*). In terms of microhabitat, *H. rubrofasciata* prefers elevated grass tussocks (*ca.* 30 cm × 30 cm) that are covered with dry leaves (Kotiaho *et al.* 2000). This preference makes *H. rubrofasciata* males easy to collect by pitfall trapping.

2. MATERIAL AND METHODS

Adult male wolf spiders, *H. rubrofasciata*, were collected by pitfall trapping from 39 natural bogs in Sipoo, southern Finland (60°16′ N and 25°14′ E) at the beginning of the mating season. After the mating season, field-mated females carrying an egg sac were collected from 25 natural bogs by hand-picking. Collected spiders were placed individually in small plastic film jars with some moss (*Sphagnum* spp.) and kept cool (*ca.* 10 °C). In the present study, we used only clearly isolated populations in bog habitats that were surrounded by forest and/or rocks. There were no streamlets or other obvious water connections between study populations. The mean distance between the 39 populations was 9.7 km. The smallest distance between two study populations was 110 m. We have observed adaptive genetic differences between populations of *H. rubrofasciata* at a very small geographical scale (Vertainen *et al.* 2000). Therefore, gene flow between *H. rubrofasciata*

populations, even those located within a few hundred metres of each other, is likely to be highly restricted.

We grouped populations into four population-size classes according to the male sampling data: I, 1–9; II, 10–29; III, 30–100; and IV, 100–10 000 or more males. In small populations (I and II), we sampled males with 50–200 pitfall traps distributed over the whole habitat for several days so as to collect all the males from the smallest populations. Pitfall traps were checked daily. In these populations, we estimated population size as the total number of males captured, because males are highly mobile during the mating season and after a few days no new males will appear in pitfalls (J. J. Ahtiainen, R. V. Alatalo, J. Mappes and L. Vertainen unpublished data). In larger populations (III and IV), we estimated population sizes by using the daily capture-rate information from 50–100 pitfall traps distributed in a restricted plot (*ca.* 10 m × 10 m). On each sampling day, we collected at least as many spiders from large populations as we collected from small populations. Overall, mortality rates in pitfall traps were very low. In the male data, there were 13 I-populations ($n = 50$ individuals; area range: 0.2–10 are, where 1 are = 100 m^2), four II-populations ($n = 81$; area range: 8–14 are), five III-populations ($n = 89$; area range: 3–7 are), and 17 IV-populations ($n = 130$; area range: 8–94 are). Females were collected from 25 out of 39 wolf spider populations. In the female data, there were seven I-populations ($n = 22$ individuals), four II-populations ($n = 37$), four III-populations ($n = 23$) and 10 IV-populations ($n = 103$).

Within a week after field collection, specimens were brought to the laboratory. Spiders were weighed to the nearest 0.1 mg with an analytical balance (AND HA-202M). Each female was weighed after her offspring had hatched from the egg sac. Females were heavier than males (females: 21.1 ± 0.3 mg; males: 16.9 ± 0.2 mg (mean$\pm$s.e.)). After body-mass measurements, males were kept individually in film jars with some moss (*Sphagnum* spp.) at $5 \pm 2\,^\circ$C, in darkness to keep their metabolic rates low. Females were kept individually in plastic vials (diameter of 28 mm, height of 67 mm) with some moss (*Sphagnum* spp.) at $22 \pm 1\,^\circ$C under natural light–dark conditions. Film jars and vials were moistened regularly, and food (*Drosophila melanogaster*) was provided *ad libitum*.

In the laboratory, we measured the sexual activity (drumming rate and mobility) of each collected male during two consecutive days. This experiment was carried out by systematically randomizing specimens into same-sized blocks. Within the blocks, there were the same number of specimens from small and large populations. Each block had approximately the same mean and variance in body mass. We placed males individually in plastic arenas (125 mm × 88 mm × 110 mm high). The bottoms of the plastic arenas were each covered with a piece of white paper (8 cm × 4 cm) glued to the bottom. For mobility measurements, each arena was divided with a line into two equal rectangles. Two dry equal-sized birch leaves were placed in the rectangles as drumming substrates. The laboratory was illuminated with fluorescent tubes, and lamps with 40 W bulbs were placed 30 cm above the floors of the drumming arenas to give extra heat and light. On the day before the onset of behavioural measurements, males were kept at the laboratory temperature ($31 \pm 1\,^\circ$C) for 2 h to trigger their sexual activity. Drumming rate was measured as the number of separate drumming bouts, and mobility as the number of times the male crossed the line between the rectangles. Drumming rate and mobility were counted during five observation periods of 2 min, and the procedure was repeated on two consecutive days. Between the trial days, males were fed with fruitflies (*D. melanogaster*) and kept in moistened film jars filled with

some moss (*Sphagnum* spp.) at $5 \pm 2\,^\circ$C. The repeatabilities for drumming rate and mobility were moderate (for drumming rate: $r = 0.318$, $F_{349,350} = 1.933$, $p < 0.001$; for mobility: $r = 0.381$, $F_{349,350} = 2.231$, $p < 0.001$) (for methods, see Krebs (1989)).

Following the sexual-activity experiment, we conducted the survival experiment for the same males (for methods, see Kotiaho *et al.* (1996), (1999), Mappes *et al.* (1996) and Kotiaho (2000)). Males of *H. rubrofasciata* were placed individually in plastic vials (diameter of 28 mm, height of 67 mm) at $22 \pm 1\,^\circ$C with continuous light and moisture. No food was provided. Male survival was recorded daily, and the number of days a male survived from the beginning of the experiment was used as the estimate of male survival. The experiment was terminated after 54 days (on 24 July), when only three males were alive.

Offspring hatched from egg sacs within a month after field-mated females were brought to the laboratory. The numbers of live and undeveloped dead offspring at hatching were determined. The number of undeveloped dead offspring was the sum of the numbers of undeveloped eggs and larva in the egg sac. Hatching success was defined as the ratio of the number of live offspring at hatching to the sum of the numbers of live and undeveloped dead offspring at hatching. The offspring body mass was calculated by averaging the body masses of three randomly chosen live offspring.

To test population-level effects, we used population means of each trait in regression analyses. All traits were normally distributed. Survival, drumming rate and mobility increased in a nonlinear fashion with increasing population size (see figure 1*a*–*c*). Therefore, we used nonlinear regressions with the S-curved model ($y = e^{(b_0 + (b_1/x))}$, or $\ln(y) = b_0 + (b_1/x)$), which gave the best coefficient of determination. There is an unpublished study that has also shown that the population-mean drumming rate increases in an S-curved manner with increasing population size in *H. rubrofasciata* (Vertainen 2001). In § 3, clutch size is presented as standardized residuals from the regression against female body mass, because *H. rubrofasciata* females with higher body masses have been shown to lay larger clutches than females with smaller body masses (Vertainen *et al.* 2000).

3. RESULTS

Population size had significant effects on survival and drumming rate (nonlinear regression, survival: $r^2 = 0.166$, $F_{1,37} = 7.37$, $p = 0.010$, $b_0 = 3.22$, $b_1 = -0.73$, $\ln(y) = 3.22 + (-0.73/x)$; drumming rate: $r^2 = 0.167$, $F_{1,37} = 7.43$, $p = 0.010$, $b_0 = 2.50$, $b_1 = -1.01$, $\ln(y) = 2.50 + (-1.01/x)$), indicating that males in larger populations (10 males or more) had both higher survival and higher drumming rate than males in the smallest populations (less than 10 males) (figure 1*a*,*b*). Populations did not differ in mobility (nonlinear regression, mobility: $r^2 = 0.052$, $F_{1,37} = 2.05$, $p = 0.161$; figure 1*c*). There was a tendency for males in small populations to have a larger body mass than males in large populations (nonlinear regression, body mass: $r^2 = 0.084$, $F_{1,37} = 3.41$, $p = 0.073$). At the individual level, there was a tendency for males with a large body mass to have a higher drumming rate than males with a low body mass (nonlinear regression: $r^2 = 0.009$, $F_{1,348} = 3.33$, $p = 0.069$). There was no effect of body mass on mobility (nonlinear regression: $r^2 = 0.004$, $F_{1,348} = 1.52$, $p = 0.219$). To assess the robustness of our results to changes in population-size classification, we pooled population-size classes I and II

and analysed the data as above. This did not change the results, implying that our results are robust.

Populations did not differ in the number of live offspring at hatching, the number of undeveloped dead offspring at hatching, hatching success, offspring body mass or female body mass (linear regression, the standardized number of live offspring at hatching: $r^2 = 0.098$, $F_{1,23} = 2.51$, $p = 0.127$; the number of undeveloped dead offspring at hatching: $r^2 = 0.003$, $F_{1,23} = 0.08$, $p = 0.782$; hatching success: $r^2 = 0.040$, $F_{1,23} = 0.96$, $p = 0.337$; offspring body mass: $r^2 = 0.001$, $F_{1,23} = 0.01$, $p = 0.907$; female body mass: $r^2 = 0.010$, $F_{1,23} = 0.23$, $p = 0.639$; table 1).

4. DISCUSSION

In this study, both male survival and drumming rate were substantially reduced in the smallest populations (less than 10 males per population) compared with larger populations of *H. rubrofasciata* (figure 1a,b). Therefore, our results provide, for the first time, to our knowledge, evidence that decreased sexual signalling reveals reduced viability in small natural populations. Our results suggest a new paradigm for integrating behavioural ecology into conservation biology by identifying male sexual signalling traits as sensitive tools to assess population viability. From a sexual-selection perspective, our results suggest that sexual signalling has important population-level consequences: females might choose male sexual traits indicative of a heritable viability to enhance the survival prospects of their offspring in small populations.

There have been only a few studies designed to investigate the effects of inbreeding on behavioural traits (Miller *et al.* 1993; Aspi 2000). Miller *et al.* (1993) have studied the effects of inbreeding on male mating ability and courtship behaviour in laboratory-reared *D. melanogaster*. Inbred males of *D. melanogaster* showed significant reductions in overall mating ability and displayed impaired mating behaviour. Aspi (2000) has shown that inbreeding decreases male courtship-song frequency in laboratory-reared *D. montana*. In *D. montana*, male courtship-song frequency is closely associated with male mating success and offspring survival (see Aspi & Hoikkala 1995; Hoikkala *et al.* 1998; Ritchie *et al.* 1998).

Obviously, females in small populations cannot afford to be choosy because of the rarity of male encounters; otherwise females might fail to breed completely. As a consequence, this might decrease population viability. Moreover, there is some evidence that female choice may increase mating skew and therefore inbreeding depression in small and isolated populations (Westemeier *et al.* 1998). Interestingly, our results show that male survival was lowered only in the smallest populations (less than 10 males) (figure 1a). Therefore, our results suggest that the indirect benefits of female choice in terms of good genes might level out the assumed viability differences in larger populations of *H. rubrofasciata* (10 males or more). A previous study lends support to this idea, as *H. rubrofasciata* females have been shown to benefit genetically through better offspring viability by choosing males with the highest drumming rates (Alatalo *et al.* 1998). Alternatively, rather than choosing good genes, females might actually avoid bad genes (i.e. deleterious alleles) by basing the information they gather on honest male signals, i.e. drumming rates. Therefore, our
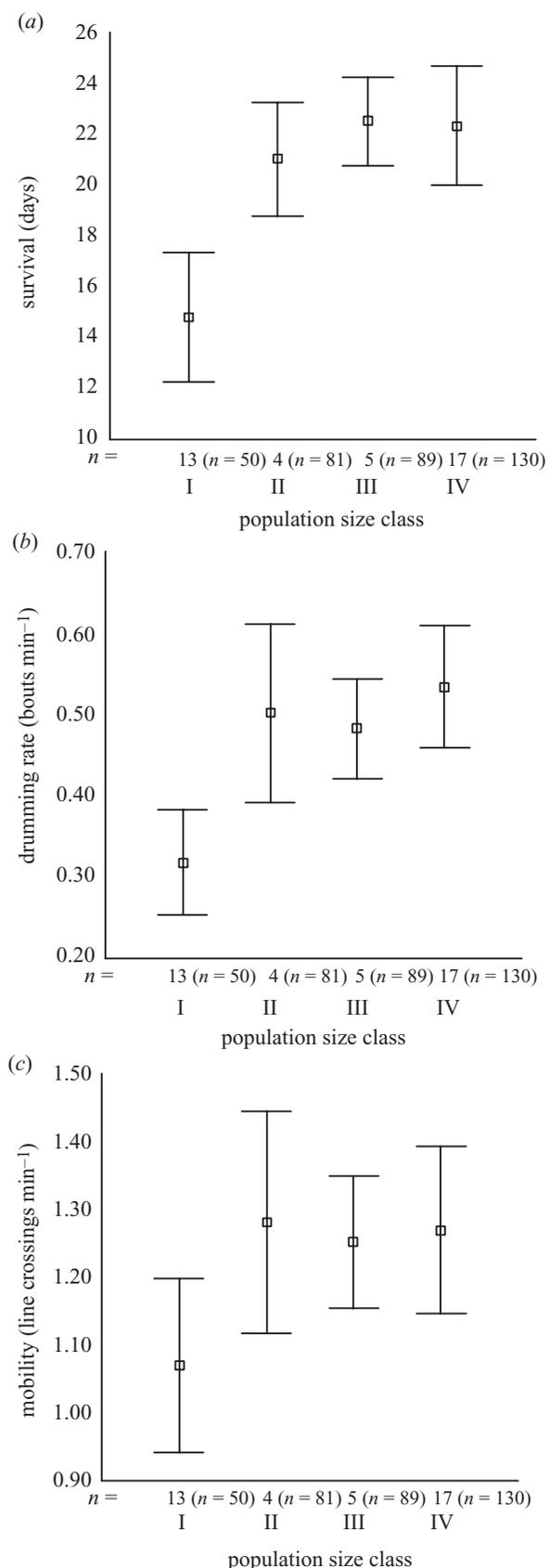

Figure 1. (a) Mean survival ($\pm$ s.e.), (b) mean drumming rate ($\pm$ s.e.) and (c) mean mobility ($\pm$ s.e.) in each population-size class. Population-size classes: I, 1–9; II, 10–29; III, 30–100; and IV, 100–10 000 or more males. The number of populations and individuals (in parentheses) in each population-size class is shown on the x-axis.

Table 1. Mean estimates of female reproductive success ($\pm$ s.e.) in each population-size class.
(Population-size classes: I, 1–9; II, 10–29; III, 30–100; and IV, 100–10 000 or more males. Hatching success is defined as the ratio of the number of live offspring at hatching to the sum of the numbers of live and undeveloped dead offspring at hatching.)

population-size class	I	II	III	IV
n (populations)	7	4	4	10
n (individuals)	22	37	23	103
the number of live offspring at hatching	26.37 $\pm$ 1.84	24.85 $\pm$ 2.21	18.29 $\pm$ 5.23	21.46 $\pm$ 1.87
the number of undeveloped dead offspring at hatching	1.16 $\pm$ 0.74	1.99 $\pm$ 0.53	1.77 $\pm$ 1.43	1.32 $\pm$ 0.42
hatching success	0.94 $\pm$ 0.04	0.90 $\pm$ 0.04	0.90 $\pm$ 0.08	0.89 $\pm$ 0.03
offspring body mass (mg)	0.51 $\pm$ 0.03	0.48 $\pm$ 0.02	0.47 $\pm$ 0.03	0.51 $\pm$ 0.01
female body mass (mg)	21.48 $\pm$ 0.85	21.00 $\pm$ 0.71	18.59 $\pm$ 1.74	21.17 $\pm$ 0.37

results suggest that, apart from in the smallest populations, sexual selection might partially compensate for the reduction in viability in small populations.

Our results did not show any effect of population size on clutch size, offspring body mass or female body mass in *H. rubrofasciata* (table 1). Therefore, a small population size does not seem to have any negative effects on female reproductive success in this species. In addition, there was a tendency for males in small populations to have higher body masses than males in large populations. Therefore, it seems unlikely that small populations of *H. rubrofasciata* were located in suboptimal habitats. Furthermore, we did not find any differences between different-sized populations in the number of undeveloped dead offspring at hatching (table 1). Also, average hatching success was high across all population-size classes. Therefore, as different-sized populations of *H. rubrofasciata* did not seem to suffer from differential mortality in embryonic development, there was no severe inbreeding depression in small populations of *H. rubrofasciata*. Polyandry could have been one confounding factor in our results, as it can decrease the costs of inbreeding (Tregenza & Wedell 2002). However, *H. rubrofasciata* females do not engage in multiple matings (J. J. Ahtiainen, R. V. Alatalo, J. Mappes and L. Vertainen, personal observation).

Our results show that there was a small population-size effect only in those traits that were expressed at the end of the *H. rubrofasciata* life history. By contrast, important early life-history traits (offspring number, hatching success and offspring body mass) did not show any decline with decreasing population size. Therefore, our results suggest that deleterious effects of small population size, if any, might be expressed at the end of the species' life history. Theoretical models and empirical studies agree with our results. They have shown that the negative fitness effects of inbreeding are expressed mainly in later life-history stages, because mildly deleterious recessive alleles are difficult to purge from the population's gene pool by natural selection (Charlesworth *et al.* 1990, 1991; Husband & Schemske 1996; Melser *et al.* 1999). The more deleterious alleles have negative developmental effects during early stages in ontogeny, which expose them to stronger purging selection (Lande & Schemske 1985; Charlesworth & Charlesworth 1990; Husband & Schemske 1996). Therefore, sexual traits may be more sensitive indicators of population viability than early life-history traits, because deleterious fitness effects of inbreeding tend to be expressed at the end of the species' life history.

The effects of sexual selection in small populations have been poorly studied, and theoretical expectations are thus somewhat speculative. Our results suggest that sexual selection may have important viability consequences at the population level. Therefore, future studies should examine viability and sexual performance in different-sized populations to test whether our results are indicative of a general pattern. In addition, future studies should analyse the genetic diversity of different-sized populations. One neat way to study the population-level consequences of sexual selection would be to swap offspring between large and small populations and examine viability and sexual performance at the adult stage. This experimental design could powerfully separate the genetic and environmental effects of population size on these traits. In conclusion, sexual traits may provide a novel sensitive tool for conservation biology to assess population viability in a global background of increasing habitat loss.

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