Sex ratio bias, male aggression, and population collapse in lizards

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The adult sex ratio (ASR) is a key parameter of the demography of human and other animal populations, yet the causes of variation in ASR, how individuals respond to this variation, and how their response feeds back into population dynamics remain poorly understood. A prevalent hypothesis is that ASR is regulated by intrasexual competition, which would cause more mortality or emigration in the sex of increasing frequency. Our experimental manipulation of populations of the common lizard (*Lacerta vivipara*) shows the opposite effect. Male mortality and emigration are not higher under male-biased ASR. Rather, an excess of adult males begets aggression toward adult females, whose survival and fecundity drop, along with their emigration rate. The ensuing prediction that adult male skew should be amplified and total population size should decline is supported by long-term data. Numerical projections show that this amplifying effect causes a major risk of population extinction. In general, such an "evolutionary trap" toward extinction threatens populations in which there is a substantial mating cost for females, and environmental changes or management practices skew the ASR toward males.

adult sex ratio | *Lacerta vivipara* | male behavior | population extinction | sexual coercion

The adult sex ratio (ASR) is a central concept of population demography (1, 2) and a key factor of evolution under sexual selection (3, 4). Recently, the issue of understanding the population consequences of ASR variation has attracted much attention from human demographers, who have become seriously concerned with the social challenges that face fast-growing populations with increasingly male-biased ASR, as in China and India (5). In nonhuman populations, ecologists and evolutionary biologists have, since the early work of Fisher (6), accepted the view that ASR fluctuations are tightly regulated (7); this has been justified primarily by assuming that ASR variation is buffered by intrasexual competition, which would cause more mortality or emigration in the sex of increasing frequency (8–11). However, although considerable efforts have been devoted to documenting the occurrence of intrasexual competition, studies of its impact on population characteristics are scant (7) and all are correlative (9, 11). Thus, whereas the need to probe the long-term social and population consequences of ASR biases has been raised repeatedly (5, 12–14), how individuals respond to ASR variation and how their response feeds back into population dynamics remains poorly understood (7, 9). Using the common lizard (*Lacerta vivipara* Jacquin 1787) as a model organism, this study provides an experimental evaluation, *in vivo* and *in silico*, of the consequences of ASR biases, scaling up from individual behavior to population dynamics.

The common lizard is a small ground-dwelling lizard in which sexes share overlapping home ranges (15). As in many other polygynous vertebrate species (9), the ASR of natural populations is often female-biased, but contrary to the classical notion of a stable ASR, substantial interannual and geographical variation occurs, which ranges from 15% to 65% males across years and populations (mean = 39% males ± 0.11 SD, $n = 33$). In the Cévennes population (located in mountainous Southern France) from which the animals used in this study originate, the mean ASR is female-biased (mean ASR = 18% males ± 0.18 SD) and varies strongly at the home range scale (data from 16 home ranges surveyed during 13 years, range = 0–0.8; $\chi^2 = 41.24$, $P = 0.0003$). In this mountainous population (15), as in other natural lowland populations (16), the mean adult mortality is usually higher in males. In general, sex differences in mortality seem to occur and vary in space and time in relation to external factors, such as climate, parasitism, or predation risk (9, 15, 16). Such natural variations in adult mortality and ASR make the common lizard an ideal model species in which to investigate the individual and population responses to an experimental manipulation of the ASR.

Materials and Methods

Experimental System. The lizards used in this study were translocated from natural populations of the Cévennes area (1,400–1,600 m above sea level, 44°30′ N, 3°45′ E) to the Ecological Research Station of Foljuif (60 m above sea level, 48°17′N, 2°41′E) during June to July 2002. Our experimental system comprised enclosed patches of habitat that offered seminatural conditions to lizards (17). Lizards were released in 12 enclosed patches (10 × 10 m) located in a natural meadow and covered by nets to avoid avian predation (18). Each enclosure was extended with a 20-m long one-way corridor ending with a pitfall trap used for daily capture of dispersing lizards. Each disperser was randomly assigned to a new, unfamiliar population of the same sex ratio treatment. The habitat configuration matches the scale and the processes of a natural patchy population, and the enclosures were large enough to support independent demographic units as in a natural metapopulation with frequent emigration and immigration events (18). In our study area, some females start reproduction after their first winter, and small females typically mate later than large females (19). Males emerge on average 1 month earlier than females, and mating occurs once per year during April and May. Eggs are laid from June through July. Females lay, on average, five transparent, soft-shelled eggs (range 1–12). Offspring hatch within one day of oviposition and are autonomous thereafter.

Sex Ratio Treatments. Our experimental sample included the three main life stages of this species (15): juveniles, yearlings (1 year), and adults (≥2 years). Each population was initiated with a similar number of juveniles (21.2 ± 0.45 SD males and 22.2 ± 1.03 SD females), six male and six female yearlings, and 18 adults. Age structure, juvenile and yearling sex ratios, and population

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Abbreviation: ASR, adult sex ratio.

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density were similar between treatments and correspond to the natural structure in populations from which the lizards originated (15). In the six female-biased populations, we released four adult males and 14 adult females (22% adult males), and we released 14 adult males and four adult females in the six male-biased populations (78% adult males). These sex ratio treatments cover the range of sex ratio variations observed across and within populations of this species.

Field Monitoring. Lizards were marked individually by toe clipping and measured for snout-vent length and body mass before release, in August 2002, in September 2002, and in June 2003. Body condition in September 2002 was measured as the body mass relative to snout-vent length in an analysis of covariance model. During each of two study periods (summer 2002 and spring 2003), individuals captured in pitfall traps at the end of a corridor were identified as dispersers, and individuals caught inside enclosures but not in pitfall traps were identified as residents. In June 2003, before oviposition started, all lizards were moved to the laboratory during several repeated capture sessions and maintained under standard conditions. An investigator unaware of the treatments counted the number of mating scars on the females' belly as well as the proportion of the back of each female that was injured. Females were classified as gravid or not, based on palpation of the abdominal cavity, and checked daily for oviposition until the end of July 2003. Fecundity (number of offspring that successfully hatched) was measured a few hours after oviposition.

Population Modeling. The long-term dynamics of ASR and population numbers were investigated by running numerical simulations of a mathematical model based on a stochastic projection matrix with two age classes (juveniles and older individuals) and a postbreeding census (2). Average model parameters were estimated from capture–recapture data recorded from 1999 to 2003 in our study populations (20). Density dependence and male aggression were described by Ricker functions (see *Supporting Text*, which is published as supporting information on the PNAS web site). Individual-based simulations included demographic stochasticity on all parameters, as well as environmental fluctuations on rates of survival and reproduction between years and populations. For the simulations, the initial population age and sex structures were similar to the ones used in this experiment. See *Supporting Text* for further detail.

Results

After introduction into the patches, individuals were allowed to disperse freely along one-way corridors that offered linear transects of habitat (18). We monitored emigration during the year following introduction. Before hibernation, the ASR treatment did not affect emigration in juveniles or yearlings (Table 3, which is published as supporting information on the PNAS web site). In adults, female emigration was higher under female-skewed ASR ($\chi^2 = 5.63$, $P = 0.02$, Fig. 1*A*), whereas male emigration did not differ between treatments ($\chi^2 = 0.12$, $P = 0.73$). There was no treatment effect on posthibernation emigration in any age or sex class (see *Supporting Text*). Thus, emigration contributed to redress the ASR skew in female-biased populations, but not in male-biased populations.

In female-biased populations, the annual mortality of males and females did not differ and yearlings and adults survived better than juveniles (logit survival contrast = 0.843 ± 0.25 SE, $P = 0.0007$, Fig. 1*B*). The absence of difference in male mortality between female-biased and male-biased populations (Fig. 1*B*) contrasts sharply with strong, age-dependent differences in female mortality (Table 1). The mortality of yearling and adult females was increased dramatically by male excess (logit survival contrast = −2.470 ± 0.05 SE, $P < 0.0001$), whereas the survival of juvenile females was not significantly affected (contrast = −0.686 ± 0.42 SE, $P = 0.10$). Considering the impact of skewed ASR on female reproductive output, we found that the proportion of gravid females was similar between treatments (logistic regression, $F_{1,10} = 0.07$, $P = 0.80$), but fecundity (number of

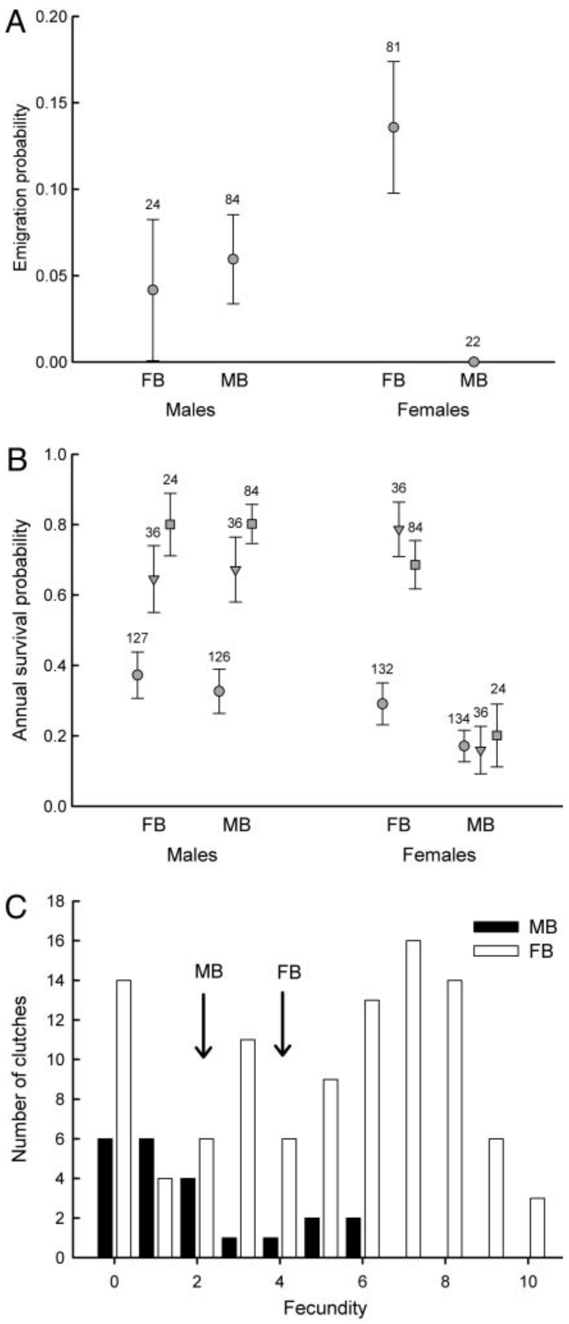

Fig. 1. Demographic consequences of the adult sex ratio manipulation. MB, male-biased populations; FB, female-biased populations. Numbers above the error bars indicate sample size. (*A*) Emigration probability in adults before hibernation (mean ± SE) per sex in each treatment. For details on statistics, see text. (*B*) Annual survival probability (mean ± SE) per age class (circle, juveniles; triangles, yearlings; squares, adults) and sex in each treatment. For details on statistics, see Table 1. (*C*) Frequency distribution of the fecundity (number of offspring that successfully hatched) in each treatment. The difference between treatments is significant (Poisson regression, treatment: $F_{1,10} = 10.24$, $P = 0.009$; effect of age: $F_{2,110} = 16.40$, $P < 0.0001$; age × treatment: $F_{2,108} = 0.08$, $P = 0.92$). Arrows indicate least-square mean per treatment after controlling for differences among age classes and populations.

Table 1. Factors affecting mortality

Term	Estimate (±SE)	Test statistic	*P*
Treatment	−0.285 ± 0.47	$F_{1,10} = 3.74$	0.08
Sex	−2.714 ± 0.40	$F_{1,860} = 29.2$	<0.0001
Age class	−1.730 ± 0.29	$F_{1,860} = 57.8$	<0.0001
Treatment × age class	0.046 ± 0.46	$F_{1,860} = 6.69$	0.01
Treatment × sex	2.755 ± 0.54	$F_{1,860} = 30.1$	<0.0001
Age class × sex	1.774 ± 0.50	$F_{1,860} = 6.59$	0.01
Treatment × age class × sex	−1.829 ± 0.67	$F_{1,860} = 7.47$	0.006
Population (treatment)	0.263 ± 0.15	$Z = 1.74$	0.04

Annual survival probability was modeled with a logistic regression including treatment, age class (juvenile, yearling, and adult) and sex as fixed factors. Population was included as a random effect nested within the treatment. The fit of the initial model was satisfying (Pearson's χ^2 GOF test, $P = 0.47$). According to the AIC criteria, a model with similar survival probabilities for yearlings and adults fits the data better than the full model (ΔAIC = 30.0). The estimates are given for female-biased populations, females, and juveniles on a logit scale.

offspring that successfully hatched) was 1.95 offspring (± 0.62 SE) lower in male-biased populations (Fig. 1*C*). Thus, male excess reduced population growth by decreasing both female survival and recruitment. As a consequence, the population size (counted after breeding) decreased from 73.2 (± 0.8 SD) to 35.3 (± 8.4 SD) in male-biased populations, whereas it increased from 73.3 (± 1.2 SD) to 118.3 (± 25.4 SD) in female-biased populations (Wilcoxon two-sample test of population growth, $\chi^2 = 8.31$, $P = 0.004$).

The lack of response to the ASR manipulation in males is congruent with results of a previous manipulation in natural populations, which found no increase in male mortality and emigration in response to higher male density (15). The negative impact of male excess on female survival and reproduction could arise from intersexual competition (21) and/or male aggression during mating (22, 23). The latter includes direct physical effects (males bite females during mating; ref. 19), stress (induced by male mating attempts) that inhibits reproduction (24), or loss of energy due to sexual harassment by males (22). Both intersexual competition and male aggression are likely to play an important role in our system, but our observations favor male aggression as a prime factor. Firstly, the number of mating scars and wounds on females due to males' biting during mating attempts were 2- to 3-fold more frequent in male-biased populations (Table 2). Secondly, we examined whether female death happened before winter or during the spring mating season (mortality during hibernation is very low in this species; ref. 25). The treatment affected posthibernation, but not prehibernation, female mortality, which supports the male aggression hypothesis (Table 4 and Fig. 4, which are published as supporting information on the PNAS web site). Thirdly, female body growth was not affected by the manipulation (Fig. 2), Lastly, prehibernation female body condition was not different between treatments (ANOVA, treatment: $F_{1,10} < 0.0001$, $P = 0.99$; age: $F_{2,315} = 12.77$, $P < 0.0001$; treatment × age: $F_{2,313} = 0.04$, $P = 0.96$). Given that females grow and accumulate their body reserves mostly during summer and autumn (15), these results suggest only weak competitive asymmetry between sexes.

Table 2. Injuries on females at the end of the mating season, in relation to treatment

Populations	Number of mating scars	Proportion of the back injured
Male-biased	3.62 ± 0.54	15.76 ± 2.05
Female-biased	1.49 ± 0.15	5.51 ± 0.80

Data are given as mean ± SE. The amount of injury on females was used to quantify the intensity of male aggression during spring (19). Males caused mating scars (U-shaped marks on the belly of females) that could be counted easily. Males mating attempts also resulted in the removal of epidermis, leading to persistent skin damage on the females' backs (scored as the proportion of back surface wounded). The effect of treatment on the number of mating scars and the proportion of wounded back was significant (respectively, Poisson regression, $F_{1,10} = 20.14$, $P = 0.001$; logistic regression, $F_{1,10} = 21.6$, $P = 0.0009$). The number of mating scars and the proportion of wounded back were not affected by the two-way interaction of treatment with age ($F_{2,142} = 1.22$, $P = 0.30$, and $F_{2,142} = 1.88$, $P = 0.16$, respectively) nor by age ($F_{2,144} = 0.73$, $P = 0.49$, and $F_{2,144} = 1.24$, $P = 0.29$, respectively).

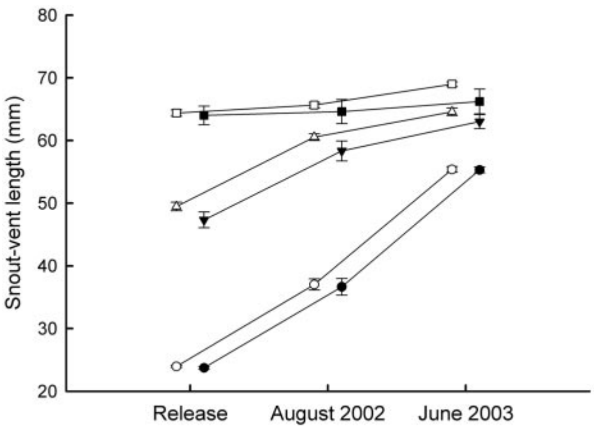

Fig. 2. Mean snout-vent length (±SE) of females in relation to treatment, age class (circle, juveniles; triangles, yearlings; squares, adults), and period. Filled symbols, male-biased populations; open symbols, female-biased populations. The trajectory of female body size was modeled with a repeated-measures model, with the measures taken at release, in August 2002, and in June 2003 as repeats. Body size was not affected by the treatment ($F_{1,10} = 1.73$, $P = 0.22$), and the two-way interactions of treatment with time ($F_{1,457} = 0.06$, $P = 0.81$), and age class ($F_{2,458} = 1.38$, $P = 0.25$), as well as the three-way interaction ($F_{2,455} = 0.85$, $P = 0.43$) were not significant. Growth rates differed among age classes ($F_{2,460} = 718.60$, $P < 0.0001$)

Higher female mortality in male-biased populations amplified the population sex ratio skew (56.5% males initially, 81% ± 3 SE after 1 year), whereas the population sex ratio remained nearly constant in female-biased populations (42% males initially, 43% ± 3% SE after 1 year). Longer-term monitoring of another set of experimental populations (18) showed similar amplification of sex ratio bias (40% initially, 61% after 4 years, $n = 16$), parallel with a sustained population decline and high extinction rates (18). Thus, the deleterious demographic effects of male excess on females raise a major threat to population persistence that had not been previously recognized (2, 13, 14). To quantify this extinction risk and to analyze its sensitivity to male and female behavior, we constructed a stage-structured stochastic population model. The model shows that stochastic sex ratio fluctuations cause a significant threat to population persistence, as expected from two-sex population theory (14, 26) (Fig. 3*A*). Indeed, in small populations of sexually reproducing organisms, demographic stochasticity impacts not only individual birth and death events, but also the offspring sex ratio. The resulting fluctuations in population sex ratio can cause occasional shortage of mates, thereby increasing the risk of population extinction.

Moreover, our model shows that the effect of stochastic sex ratio fluctuations on extinction risk is dramatically amplified by male aggression (Fig. 3 *A* and *B*): compared to the one-sex model, the extinction risk of an isolated population increases with projection time about twice as fast in the two-sex model, and 10 times faster in the two-sex model that includes male aggression. The initial ASR skew has little effect on this pattern (Fig. 3*A*). The demographic dynamics of the population on its way to

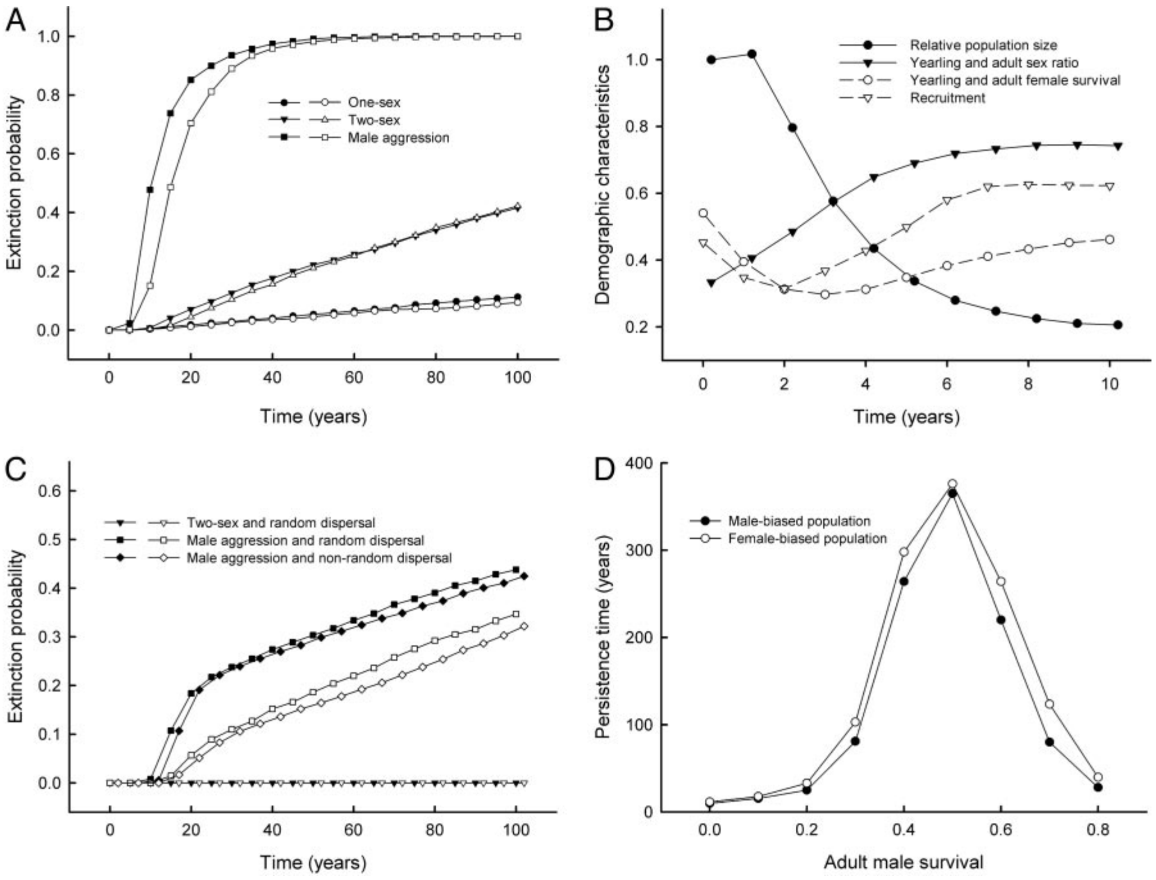

Fig. 3. Adult sex ratio, male aggression, and population extinction risk. See supporting information for model construction and analysis and all parameter values. (*A*) Cumulated extinction probability over time of an isolated population, as predicted by a one-sex model, a two sex-model without male aggression, and a two-sex model with male aggression. Filled symbols, initially male-biased populations; open symbols, initially female-biased populations. (*B*) Demographic dynamics during extinction in the two-sex model with male aggression, as predicted for an isolated, initially female-biased population. Data shown are population size (scaled to its initial value), yearling and adult sex ratio, yearling and adult female survival, and recruitment (number of female offspring per female) conditional on nonextinction (2). (*C*) Cumulated extinction probability over time as predicted by a two-sex metapopulation model in the absence of male aggression, with male aggression and random emigration, or with male aggression and female emigration in response to higher local density of females. All results are based on Monte Carlo simulations of 2,000 trajectories. Filled symbols, initially male-biased populations; open symbols, initially female-biased populations. (*D*) Evolutionary trap: nonmonotonic response of median persistence time (Monte Carlo simulations of 2,000 extinct trajectories) to increasing adult male survival as predicted by a two-sex metapopulation model with male aggression and female emigration in response to higher local density of females. Population viability is maximized for adult male survival probabilities similar to the ones observed in wild populations from which the lizards originated (15). Population viability is also higher when the initial ASR is female-biased.

extinction is revealed by Fig. 3*B*. In a first phase, recruitment and adult female survival drop as an immediate consequence of male aggression, which both increase the population sex ratio skew toward males and decreases population size. Thereafter, recruitment and survival respond to the negative effects of more aggression (due to a more male-biased population sex ratio) and the positive effects of less competition for resources (due to lower population size). In a second phase, conditional on nonextinction of the populations, these conflicting factors have a positive net effect on recruitment and survival. However, remnant populations are then reduced to small size, which results in their rapid extinction under the effects of demographic and environmental stochasticity (Fig. 3 *A* and *B*). Extending our model to account for habitat fragmentation and individual dispersal further shows that adult female emigration from female-skewed patches does not buffer the demographic effects of male aggression (Fig. 3*C*). However, in this case, populations with an initially female-biased ASR have a lower chance of extinction. These population projections are robust to changes in salient parameters and structural features of the model (see Figs. 5 and 6, which are published as supporting information on the PNAS web site).

Discussion

Population and evolutionary theory has long relied on the hypothesis of ASR stability, and thereby kept the issue of ASR dynamics largely out of the spotlight (2, 12–14). Our results demonstrate that ASR dynamics can have profound consequences for individual behavior and ultimately for population dynamics. Contrary to the common expectation that behavioral responses to ASR variation should stabilize the sex structure of animal populations, our experimental manipulation of lizard populations and the numerical simulations of their long-term dynamics showed that sexual aggression by males can rapidly amplify male bias and cause population collapse. Thus, the male behavior described here is harmful to females and severely threatens population viability.

In many sexually reproducing species, individuals of one sex (typically males) compete for access to mating partners, whereas individuals of the other sex (typically females) choose between partners of the opposite sex and compete for food resources (8). Fluctuations in the ASR are central to predicting the intensity of competition for mates and resources (3, 4). However, there is little information available on how ASR-mediated changes in social behavior can influence reproductive effort and demographic performances in males and females (27). According to the prevailing theory of intrasexual competition (8), we expected higher reproductive effort and poorer demographic performances in the sex of experimentally increased frequency. In contrast, demographic performances (measured by survival) of male lizards were not affected by the ASR manipulation. Rather, male excess resulted in increased levels of sexual aggression against females, whose survival, birth, and emigration rates dropped. A previous study in natural populations of the common lizard demonstrated intrasexual competition for food among females (15). Thus, the results of the present manipulation indicate that effects of males on females in response to the ASR perturbation were disproportionate compared to competition among females for food.

The behavior of males toward female conspecifics demonstrated by this experiment is a likely evolutionary outcome of a sexual conflict over mating and reproduction tactics, which has led to adaptations which benefit males (in the short term) but not females (28, 29). Sexual coercion (e.g., forced copulation, sexual harassment, and punishment), as it has been termed, has been recognized as one of the key forces of sexual selection along with mate choice and mate competition (23). Sexual coercion seems to be widespread in insects and other invertebrates, where it involves sexual harassment by males and causes survival and lifetime reproductive costs to females (30). For example, in seed-eating true bugs, harassment can reduce fecundity by up to 50%, and females are seen to leave prime oviposition sites when males are abundant (31). Although less is known about the fitness costs of such behaviors in vertebrates, several observations suggest that harassment by males may be common, with potentially substantial fitness consequences for females (23, 32). In fish, females can be harassed by males and suffer reduced foraging time at male-biased ASRs (22). In the Australian quacking frog (*Crinia georgiana*), females that are amplexed by several males risk asphyxia, and struggles between males reduce fertilization success (33).

Despite these dramatic empirical observations, population theory remains strongly female-focused and the role of males in the population dynamics of animal species has chronically been underestimated (34). In fact, males and females often differ in their vital rates, density dependence, and sensitivity to the environment (9). Nonmanipulative studies have identified possible consequences of sex structure on population dynamics (9, 11), including reproductive collapse after male rarity (13). By experimental manipulation, long-term monitoring, and mathematical projections of populations of common lizards, we demonstrate rigorously that male-biased ASRs exacerbate male aggression and become deleterious to females, which amplifies further the sex ratio biases toward males and leads to a positive feedback of population decline, that is, an extinction vortex. For example, it is suspected that attacks by adult males on females, occurring under a male-biased ASR, are a major threat to population persistence of the Hawaiian monk seal (*Monachus schauinslandi*) (35). In other species, social dominance, reproductive suppression, and infanticide are behaviors of adult males that similarly erode female fitness (21, 36); these effects should be aggravated by male-biased ASRs.

Large fitness rewards of aggression for males (23) and limited effectiveness of natural selection in rapidly declining populations (37) may explain why counteradaptations in females (38) (e.g., emigration in response to male excess) did not evolve in this species, even though dispersal by its individuals responds adaptively to a wide range of social and demographic cues (20). Thus, local populations of the common lizard face an "evolutionary trap" (a maladaptive response to sudden environmental change that causes rapid extinction, see ref. 39) into which they are likely to fall in response to increasing male survival (Fig. 3*D*). An improvement of environmental conditions during spring, e.g., due to climate warming, may reduce male-biased spring mortality (e.g., in *L. vivipara*; ref. 15) and thereby induce male-biased ASRs. Climate warming could also have an indirect impact on ASR by altering common lizard sex-specific phenology and their predators' phenology (40). Generally, the population viability of many vertebrate species with potentially high mating costs in females (23) and in which ecological factors naturally cause lower survival in adult males (9) may be affected by population sex-ratio deviations. Hence, human impact on factors affecting male survival, through population management (9) or large-scale environmental changes (40), may induce or enhance ASR male bias, aggravate male aggression, and therefore close the evolutionary trap.

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