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Sexual conflict over habitat selection: the game and a test with small mammals

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ABSTRACT

Background: Sexual conflict arises when the evolutionary strategies of reproduction by one sex differ from those of the other. The differences in evolutionary strategies are often associated with sexually antagonistic selection and an arms war of adaptation and counter-adaptation between the sexes. The selection gradient will disappear, and resolve the conflict, if fitness trade-offs between the sexes allow them to achieve equal fitness.

Questions: Does density-dependent habitat selection resolve sexual conflict? Can we use the sex ratio in a habitat to assess sexual conflict?

Mathematical methods: Isodar theory, two-by-two matrix games, and computer simulation.

Field methods: Manipulation of food supplements provided to a controlled population of meadow voles (*Microtus pennsylvanicus*) living in rodent-proof interconnected field enclosures. Use of remote antennae to monitor habitat use by radio-frequency identification-tagged male and female voles.

Key assumptions: Sexual conflict occurs in meadow voles. Relative use of interconnected habitat enclosures by male and female voles can evaluate habitat-dependent sexual conflict. All individuals have equal effects on resource consumption. Fitness is equalized between habitats by population density. Female fitness is increased by mate choice and reduced by male harassment. Male fitness depends on mating success and female fitness.

Conclusions: When male and female fitness varies between habitats, density- and sex-dependent habitat selection resolve sexual conflict. The sexual conflict game is typified by dominant strategies for both males and females that create local differences in sex ratio. Sex ratios of meadow voles using five enclosures confirmed the theory's predictions. The local sex ratio was male biased (there were always more males using an enclosure than females) even though the global sex ratio was 1 : 1.

Keywords: fitness, habitat selection, isodar, matrix games, sex ratio, sexual conflict, voles.

INTRODUCTION

Although males and females must cooperate for sexual reproduction, their best reproductive strategies to maximize fitness frequently conflict with one another (Parker, 1979; Arnqvist and Rowe, 2005). Less appreciated, perhaps, are additional ecological conflicts that arise over habitat

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selection through the need to secure the resources and space that each sex requires for its separate mating, reproductive, and survival options (but see Bowyer, 2004, as well as Ruckstuhl and Neuhaus, 2006). These differences between the sexes in habitat requirements are especially interesting because they are likely to interact with operational sex ratios and mating strategies.

The fitness that an individual can expect to attain in a habitat depends on the density of other individuals already present (Fretwell and Lucas, 1969; Rosenzweig, 1981). Although most theories state that fitness declines with increased density, positive density dependence, particularly in small populations, can emerge from biased sex ratios that reduce mating opportunities for the least abundant sex [Allee effects (Allee, 1931)]. Positive density dependence is much less likely at moderate population densities because stochastic processes will have less ability to produce skewed sex ratios. It is nevertheless reasonable to anticipate that the optimum sex ratio is different for males than it is for females, and that conflict over that ratio will be played out through differences between the sexes in density-dependent habitat selection.

We explore these ideas in three ways: First, we modify theories of density-dependent habitat selection so that each sex can separately adjust its use of habitat relative to intrinsic habitat quality, density, and the proportional occupation of the habitat by members of each sex. Second, we use computer simulations to illustrate that although it is possible for the population to achieve simultaneously stable spatial distributions of density and sex ratio, it is much more probable that the conflict cannot be uniquely resolved and that it will wax and wane with changes in population size. Third, we test the theory with controlled reciprocal experiments that manipulated resource renewal for voles between otherwise similar pairs of habitats. The experiments document density-dependent habitat selection by males and females, that the sex ratio depends on local population density, and that it emerges through density-dependent variation in male home-range size.

GAMES OF HABITAT SELECTION

Theory

Our theory makes the following assumptions: (1) individuals reproduce sexually and are promiscuous; (2) there is no paternal care; (3) individuals are monomorphic sexually mature virgin adults equally receptive to mating; (4) metabolism is similar between males and females; (5) individual fitness declines linearly as density increases [we acknowledge the existence of Allee effects (Allee, 1931), where population growth rate increases with density at low population size, but assume, for modelling purposes, that the range of applicable densities always exceeds those with positive density-dependence on fitness].

Imagine that the population grows according to the Ricker (1954) equation

$$N_{i(t+1)} = N_{i(t)} e^{r\left(1 - \frac{N_{i(t)}}{K_i}\right)} \tag{1}$$

where N is population density (= population size in equally sized habitats) in habitat i at times t and $t + 1$, r is the maximum instantaneous rate of population growth at low density, and K is the habitat's carrying capacity. Rearranging equation (1) yields the per capita rate of population growth (our estimate of fitness):

$$\ln(N_{i(t+1)}) - \ln(N_{(t)}) = r_i - \frac{r_i}{K_i} N_i . \tag{2}$$

If we consider a landscape composed of two habitats, then the solution at equilibrium when the fitness in habitat 2 is equal to that in habitat 1 (Fretwell and Lucas, 1969) is given by the population's habitat isodar, the set of densities in the two habitats such that expected fitness is equal (Morris, 1987, 1988):

$$N_2 = \frac{r_2 - r_1}{r_2} K_2 + \frac{K_2}{K_1} \frac{r_1}{r_2} N_1 . \tag{3}$$

Within these broad constraints, however, the fitness of males and females might differ (and hence strategies of habitat selection) if the 'residual fitness' associated with being either male or female is influenced by sex ratio. We first consider a landscape composed of large patches of a single habitat in inhospitable matrix and assume that a female's residual fitness following density-dependent habitat selection (density equal in all habitat patches) increases with opportunities for mate choice, but declines with male harassment. We further assume that females require a minimum threshold of males (N_{imT}) (at least two) before the advantages of mate choice can take effect. For simplicity, we imagine that the same threshold is required before females begin to be harassed by males. Thus, beyond the threshold, residual fitness associated with opportunities for mate choice increases with the ratio of males to females, as does the cost of male harassment. A female's residual fitness given that the population density in a patch is determined by density-dependent habitat selection is thus

$$W_{ifr} = \theta_i \frac{N_{im}}{N_{if}} \bigg| \; N_{im} > N_{imT} \tag{4}$$

where the subscripts f and m identify females and males respectively, W_{ifr} represents the residual fitness females accrue via mate choice in habitat i, and θ is the net difference in fitness accrued through the benefit of mate choice and the cost of harassment [assumed to have the same sign in all habitats (female survival during reproduction is implicit in θ)].

A male's residual fitness is linked directly to the fitness of his female partners and will therefore depend on the probability that the male survives through the mating season, the number of mates that he obtains, and the fitness of those mates. We assume that mating success is proportional to the ratio of receptive females relative to males. Thus male fitness in i can be modelled as

$$W_{imr} = s_i \left(\frac{N_{if}}{N_{im}} \right) W_{ifr} \tag{5}$$

where s is the probability of male survival while females are receptive to mating, and the ratio of eligible females to males is the expected number of mates.

Setting male and female fitness equal to resolve sexual conflict, the number of males in habitat i is given by its sex-ratio isodar

$$N_{im} = s_i N_{if} \qquad \text{and} \qquad N_{im}/N_{if} = s_i \tag{6}$$

The equilibrium sex ratio of successfully reproducing animals will thus be biased in favour of females whenever the probability of male survival through the mating period is less than 1.

We now explore the consequences that emerge when the balance between mate choice and sexual harassment, as well as male survival, differ between two habitats. Setting female fitness (equation 4) equal between the habitats yields the female isodar

$$N_{2m} = \left(\frac{N_{1m}}{N_{1f}} \frac{\theta_1}{\theta_2} \right) N_{2f} \tag{7}$$

and the male isodar emerges by subsequently setting male fitness equal between habitats (equation 5, note that this assumes females have equalized their fitness between habitats),

$$N_{2m} = \left(\frac{N_{1m}}{N_{1f}} \frac{s_2\theta_2}{s_1\theta_1} \right) N_{2f}. \tag{8}$$

Males and females will thus agree on a habitat's equilibrium sex ratio only when the product of male survival multiplied by the net benefit of females in habitat *j* is equal to the net female benefit in habitat *i*. Otherwise, the isodar planes never intersect (Fig. 1), and males and females will be in conflict over a habitat's optimum sex ratio.

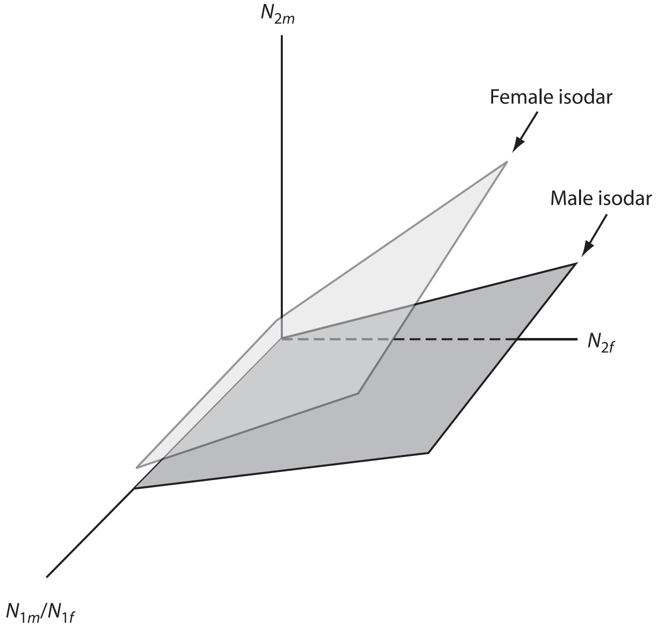

Fig. 1. Isodars illustrating sexual conflict over habitat selection. Female fitness is maximized along the light upper plane whereas male fitness is maximized along the dark lower one. The intercept of the female isodar corresponds to the threshold density of males (equation 4) necessary to invoke an advantage from mate choice. The isodar planes will rarely overlap if habitats differ in male survival and net benefits to females (equations 7 and 8). Females, in this example, prefer a higher proportion of males in habitat 2 than do males.

Computer simulations of the ‘sexual-conflict over habitat selection’ game

Conflict over the optimum sex ratio does not necessarily mean that the habitat occupation strategy is different for males than it is for females. To visualize this apparently paradoxical outcome, we modelled the conflict as an asymmetric, simultaneous two-player matrix game (Fig. 2). An individual of each sex could play one of two pure strategies without cost: remain in habitat 1 or move to habitat 2. We assumed equal areas for both habitats, specified that habitat 2 had a higher population growth rate at low density than did habitat 1, and examined the outcomes in terms of habitat selection across a broad range of parameter values.

We established the starting densities for each game by calculating the ideal-free distribution of individuals for each set of parameter values. We calibrated payoffs across a range of different sex ratios in each habitat. We did this by varying the sex ratio in habitat 1, and then calculated the sex ratio that must exist in habitat 2 to maintain both the population-wide sex ratio and an ideal-free distribution of individuals. Payoffs for each strategy included the change in density and sex ratio caused by the other player’s habitat choice. The payoff for the male, if he stayed in the original habitat, depended on the female’s strategy and vice versa. If the female stayed in the patch, total density was increased by 2 (both individuals remained), and the density of each sex increased by 1. If the female departed, the density was incremented by a single individual (the male) and his payoff depended on the original density of females living in the same habitat. Female payoffs were calculated similarly.

Each ‘simulation’ assessed the best strategy that an additional individual of each sex should follow according to the payoffs associated with its ‘opponent’s’ habitat choices. Our intent was to assess whether male and female habitat-selection strategies yielded biased sex ratios in the two habitats. Accordingly, we report outcomes only for growing populations ($N_1 = K_1/2$) with initial 1:1 sex ratios (proportion of males, $R, = 0.5$) in both habitats. Inspection of the payoffs in Fig. 2 suggests that males and females will often play opposing dominant strategies (e.g. females stay in habitat 1 while males move to habitat 2) that skew the sex ratios in each habitat away from the population mean. The sex ratio will remain equal, however, if each sex plays the same strategy (stay in habitat 1 or move to habitat 2). Our objective is to evaluate whether reasonable combinations of fitness parameters produce sexual conflict over habitat selection. We are not interested, at this time, in exploring the full range of possibilities, or whether the sex ratios we discover represent an evolutionarily stable strategy of sex-dependent habitat selection.

We begin by mimicking a game similar to that reported for male and female Trinidadian guppies (Croft *et al.*, 2006; Magellan and Magurran, 2006; Darden and Croft, 2008) in which females preferentially occupy habitats where predation on males is high, and harassment from males is reduced. The outcome of this game yields opposing pure strategies: the female prefers to stay in the male’s risky habitat where she faces less harassment while the male prefers to move to the safer one (Table 1, trial a). The strategies are similar even at a sex ratio of 4:1, but only the male plays a dominant strategy (move regardless of the female’s strategy, trial b). The outcome of the game depends on the magnitude of the trade-offs. Sex ratios remain constant (both sexes stay in habitat 1) when male survival there approaches that in habitat 2 (Table 1, trial c). If the densities are low enough, however (e.g. $N_1 = K_1/10$), dominant, repeating strategies reappear (female stays, male leaves, not shown).

We were particularly interested in the outcomes of simulations that best represent the experimental meadow-vole model that we used to test the theory. Female meadow voles

		Male choice	
		Stay in H_1	Move to H_2
Female choice	Stay in H_1	$s_1\dfrac{(N_{1f}+1)}{(N_{1m}+1)}\left(r_1-\dfrac{r_1}{K_1}(N_1+2)+\theta_1\left(\dfrac{N_{1m}+1}{N_{1f}+1}\right)\right)-D(N_{1f}+1)$ $r_1-\dfrac{r_1}{K_1}(N_1+2)+\theta_1\dfrac{(N_{1m}+1)}{(N_{1f}+1)}-B(N_{1m}+1)$	$s_2\dfrac{(N_{2f})}{(N_{2m}+1)}\left(r_2-\dfrac{r_2}{K_2}(N_2+1)+\theta_2\left(\dfrac{N_{2m}+1}{N_{2f}}\right)\right)-D(N_{2f})$ $r_1-\dfrac{r_1}{K_1}(N_1+1)+\theta_1\dfrac{(N_{1m})}{(N_{1f}+1)}-B(N_{1m})$
	Move to H_2	$s_1\dfrac{(N_{1f})}{(N_{1m}+1)}\left(r_1-\dfrac{r_1}{K_1}(N_1+1)+\theta_1\left(\dfrac{N_{1m}+1}{N_{1f}}\right)\right)-D(N_{1f})$ $r_2-\dfrac{r_2}{K_2}(N_2+1)+\theta_2\dfrac{(N_{2m})}{(N_{2f}+1)}-B(N_{2m})$	$s_2\dfrac{(N_{2f}+1)}{(N_{2m}+1)}\left(r_2-\dfrac{r_2}{K_2}(N_2+2)+\theta_2\left(\dfrac{N_{2m}+1}{N_{2f}+1}\right)\right)-D(N_{2f}+1)$ $r_2-\dfrac{r_2}{K_2}(N_2+2)+\theta_2\dfrac{(N_{2m}+1)}{(N_{2f}+1)}-B(N_{2m}+1)$

Fig. 2. An asymmetric matrix game of sexual conflict over habitat selection. The two players represent one male and one female faced with simultaneous choices either to remain in habitat 1 or move to habitat 2. Payoffs to males are given in the top equation in each cell; payoffs to females are given by the lower equation. Payoffs correspond to the fitness expected for each player given the opponent's strategy. Symbols correspond with those in equations (2), (4), and (5). *B* represents the density-dependent reduction in female fitness associated with male density; *D* corresponds to density-dependent reduction in male fitness associated with female dominance.

Table 1. Examples of movement decisions for males and females obeying an ideal-free distribution (IFD) with differences in sex ratios, harassment, survival, benefits, and dominance (according to the payoff equations illustrated in Fig. 2)

Trial	R_1	Harassment	Male survival	Per capita benefits	Per capita dominance	Female choice	Male choice
a	0.5	$\theta_1 = -0.01$, $\theta_2 = -0.02$	$s_1 = 0.7$, $s_2 = 1$	$B = 0$	$D = 0$	**Stay***	**Move***
b	0.8	$\theta_1 = -0.01$, $\theta_2 = -0.02$	$s_1 = 0.7$, $s_2 = 1$	$B = 0$	$D = 0$	Stay*	**Move***
c	0.5	$\theta_1 = -0.002$, $\theta_2 = -0.01$	$s_1 = 0.9$, $s_2 = 1$	$B = 0$	$D = 0$	**Stay**	**Stay**
d	0.5	$\theta_1 = 0.01$, $\theta_2 = 0.01$	$s_1 = 1$, $s_2 = 1$	$B = -0.0001$	$D = 0.0005$	**Move***	**Stay***
e	0.5	$\theta_1 = 0.02$, $\theta_2 = 0.01$	$s_1 = 0.7$, $s_2 = 1$	$B = -0.0001$	$D = 0.0005$	**Stay**	**Stay**

Note: Stay = remain in habitat 1, move = move to habitat 2. All options were evaluated at the IFD with $r_1 = 0.1$, $r_2 = 0.2$, $K_1 = 100$, $K_2 = 200$, $N_1 = 50$ and a population sex ratio of 1 : 1. Dominant strategies are identified with **bold** text. *Skewed sex ratios at equilibrium.

choose some males over others, males possess several traits in conflict with female evolutionary interests (below), laboratory experiments document that females are at least as aggressive as males, and males and females engage in agonistic as well as non-agonistic interactions (McElman and Morris, 1977). It seems likely, therefore, that any benefits (*B*) from mate-choice that females accrue with male-biased sex ratios likely deteriorate with male density. We modelled this effect by including a negative density-dependent term in the calculation of female fitness (we assumed that all males had the same cumulative effect, *B*). Reproducing female meadow voles maintain exclusive territories (Madison, 1980, 1985), so we included a density-dependent cost for male interactions (*D*) with females. We examined the influence of these two density-dependent effects in subsequent simulations.

Again, an equal sex ratio in the two habitats is unstable (Table 1, trial d). Females and males play opposing dominant strategies. Indeed, females play a dominant strategy at all of the sex ratios we investigated (leave if $R_1 \leq 0.5$, stay if $R_1 \geq 0.6$, not shown). Males play a contrary dominant strategy at most sex ratios (stay if $R_1 \leq 0.5$, leave if $R_1 \geq 0.7$; but leave only if females also leave, and stay if females stay at $R_1 = 0.6$, not shown). As demonstrated above, the players' strategies, but not the game's outcome, depend on population density. Both sexes play opposing dominant strategies across the range of sex ratios that we simulated. Under each scenario, the sex ratio in habitat 1 (lower density and lower quality) will be biased towards males, and that in habitat 2 (higher density and higher quality) towards females.

There are, of course, combinations of parameter values that yield stable 1 : 1 sex ratios in each habitat (Table 1, trials c and e). We were unable to simulate, with these payoffs, a true 'battle of the sexes' where neither sex played a dominant strategy and preferred a different outcome from the other.

A TEST OF SEXUAL CONFLICT OVER HABITAT SELECTION

Model system

We searched for sexual conflict over habitat selection between male and female meadow voles (*Microtus pennsylvanicus*), a small herbivore with multiple paternity (Boonstra *et al.*, 1993; Berteaux *et al.*, 1999) and well-described density-dependent habitat selection (Pusenius and Schmidt, 2002; Lin and Batzli, 2004; Oatway and Morris, 2007, Morris and MacEachern, in press. Meadow voles appear to select habitat according to an ideal-free distribution except at high population densities where dominant individuals interfere with the habitat choices of subordinates (Pusenius and Schmidt, 2002). There is also convincing evidence of sexual conflict between male and female meadow voles that corresponds closely with our general model. Females are promiscuous, express mate choice (Berteaux *et al.*, 1999), and are aggressive towards strange males (Webster *et al.*, 1981; Boonstra 1984). Male meadow voles can block or disrupt pregnancy (Clulow and Langford, 1971; Storey, 1994), engage in sperm competition (delBarco-Trillo and Ferkin, 2006) as well as infanticide (Webster *et al.*, 1981), and produce copulatory plugs (Baumgardner *et al.*, 1982) that likely enhance paternity.

We tested the theory in the Lakehead University Habitron, a series of adjacent square enclosures in a mixture of old fields and alder forest in northern Ontario, Canada. Each enclosure is surrounded by vole-proof, galvanized metal fences with circular, ground level gates (9.25 cm diameter) that can be opened to allow dispersal to and from an adjacent enclosure, or closed to eliminate it. We used one large enclosure (50 × 50 m) that has two equidistant gates on each side, and four small enclosures (25 × 25 m squares) with a single gate on each side (Fig. 3). Each enclosure was composed of a similar old-field habitat with interspersed red-pine (*Pinus resinosa*) saplings 2–3 m tall. Voles were present only in the small enclosures when we initiated the experiment.

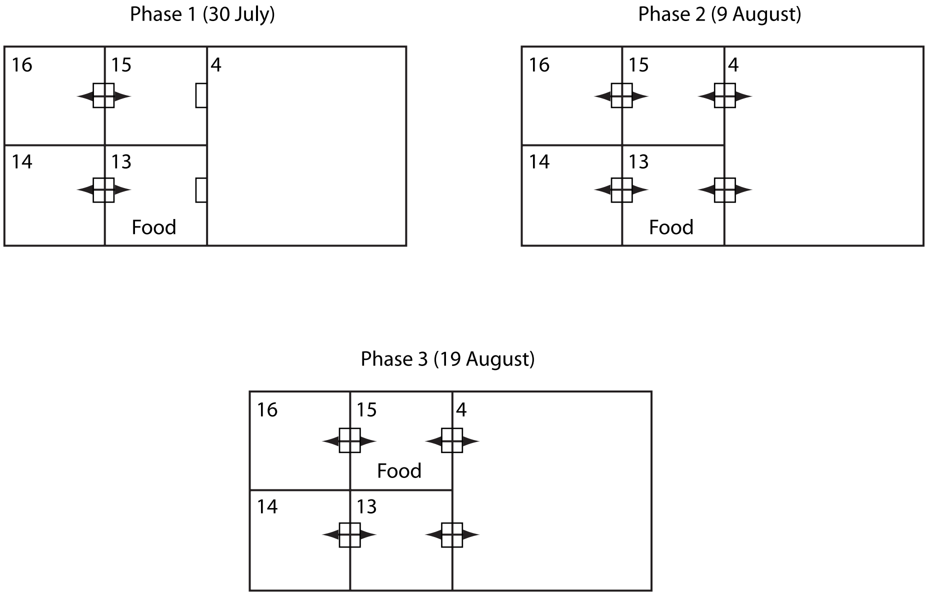

Fig. 3. Schematic representation of the three phases of the experimental design testing for sexual conflict over habitat selection by meadow voles occupying four enclosures of equal size in the Lakehead University Habitron in northwestern Ontario, Canada. Small rectangles represent antennae recording the use of enclosures by voles with radio-frequency identification (RFID) tags. Double-headed arrows signify open gates allowing voles to move between adjacent enclosures. Numbers identify different enclosures and the initiation dates of each of the three experimental phases are in parentheses. Phase 1 established reference densities, so only data from phase 2 and phase 3 of the design were used to assess sexual conflict.

We live-trapped voles (five baited metal traps placed at approximately 1–2 m intervals at each of four stations arranged as a 12.5 m grid within each small enclosure; maximum of 80 traps) for a total of 6 days in July 2008 while the gates were closed, and recorded each animal's sex, age, and body mass before injecting each one with a unique radio-frequency identification (RFID) tag. We did not inject animals weighing less than 15 g and removed them from the experiment. We opened gates to allow the 78 RFID-tagged adult voles an opportunity to choose among six interconnected small enclosures for a total of 24 days before re-closing all gates to initiate the experiment in four of the enclosures containing remote antennae that recorded RFID tags. The animals in our experiment were thus 'self-selected'. Voles that chose the two excluded enclosures were not used in the experiment.

Experimental design

The theory applies only to density-dependent habitat selectors so we built our test around another experiment designed to confirm that the voles selected habitat in a density-dependent manner (Morris and MacEachern, in press). We created a rich enclosure (Habitron small enclosure 13) by broadcasting sunflower seeds (in an approximately 5 m radius) and alfalfa cubes (along 5 m transects) at each trapping station every 2 days. The two food supplements were sufficient to supply the entire energetic demand of 39 lactating meadow voles (Morris and MacEachern, in press). We removed all juveniles and allowed the RFID-tagged adult voles to move among enclosures for 7 days. We closed the gates and set live traps again while we removed juveniles for 2 days, then re-opened the gates and switched our supplemental feeding to a different enclosure (small enclosure 15) for the remainder of the experiment (33 days).

We monitored the relative use of each habitat with four pairs of automated RFID antennae (Vantro Systems, Burnsville, MN, USA) placed on opposite sides of each open gate. Each antenna was attached to a data logger that recorded the identity, date, and time (± 1 s) whenever a tagged vole crossed over the antenna. We downloaded these data into a laptop computer every 2 days when we recharged the treatment enclosure with supplemental food. We summarized these data as the number of marked animals using each of the enclosures each day.

We also placed one pair of artificial food patches (8 g of whole oats mixed in 1.5 litres of sieved silica sand) in each small enclosure, and four pairs in the large one. Each enclosure thus had an equal density of additional food patches that we also recharged every 2 days (part of a different experiment). We used only data accumulated from antennae located at gates to determine which marked animals occupied each enclosure.

Our test of the theory assumes that voles are density-dependent habitat selectors. If they are, then the number of our marked voles should have been high in enclosure 13 while food was added there, and should have declined when we quit adding food. Meanwhile, the number of marked voles should have been low in enclosure 15 while food was provided in enclosure 13, and should have increased when we switched supplemental feeding to enclosure 15. Meadow voles obeyed both predictions (Morris and MacEachern, in press). *Microtus pennsylvanicus* in our experiments selected habitat according to density.

We tested for sexual conflict by plotting the sex-ratio isodar of the RFID-tagged meadow voles. Data for the isodar were based on the number of male and female voles recorded in an enclosure during each 24 h cycle. Animals did not have 24 h access to our antennae on the first day of the experiment (gates opened at noon), or on the days when we live-trapped and removed juveniles. We excluded these data from the analysis. The final 40-day data set provided a wide range of densities for the isodar because voles changed their distribution (and thus density in an enclosure) through time as they tracked the supplemental food experiment (Morris and MacEachern, in press). We reasoned that if the fitness of males and females varies between sexes and habitats, then the sex ratio should vary with changes in the density of individuals occupying an enclosure (equations 7 and 8). Otherwise, the linear sex-ratio isodar should pass through the origin with a slope of 1 in this monomorphic species.

Our analyses demonstrate that more males than females occupied enclosures with few females, but that the number of males and females was approximately equal when many females occupied an enclosure. We were curious to identify the mechanism responsible for this pattern. Differences in habitat use between the sexes must be related to differences in their use of space because we had marked equal numbers of male and female voles. We tested this idea by estimating average ‘home-range size’ as the mean number of enclosures used separately by males and females during each of the 40 days of the experiment. We tested whether the mean home range sizes of males and females were different, then asked whether they changed through time. We predicted a reduction in mean home range size as the animals became more accustomed to our feeding supplements.

Our design has the potential for a significant flaw. If the vast majority of animals were to occupy only the rich enclosure, then the sex-ratio isodar would necessarily converge on unity at these high densities because the initial number of marked males and females was identical. Meanwhile, if males maintained larger home ranges than females, the isodar would be male-biased in the remaining ‘low-density’ enclosures. We attempted to reduce this possible bias by ensuring that our supplements were sufficient to support only about one-half of the experimental population, and by assessing whether home-range size remained constant for the duration of the experiment.

RESULTS

The sex ratio of marked voles was 1 : 1

We placed RFID tags in all eligible voles, regardless of sex. Our final sample, nevertheless, was evenly distributed between males and females (39 marked individuals of each sex). This result is consistent with other studies that reported equal sex ratios for wild populations of meadow voles (Boonstra, 1989; Lin and Batzli, 2001), but there are some exceptions (e.g. Nadeau, 1985; Rose and Kratimenos, 2006).

The sex-ratio isodar documented sexual conflict over habitat selection

The number of male voles recorded in an enclosure was positively related to the number of females in that enclosure ($F_{1,198} = 145.06$, $P < 0.001$; Fig. 4). Males were more abundant, by a constant amount (about four individuals), than females at all densities (geometric mean regression, 95% confidence interval about the intercept = 2.67–4.56, 95% confidence interval of the slope = 0.94–1.16). The significantly higher densities of males in a habitat than females, despite an equal sex ratio, must have occurred through the differential use of space by male and female voles.

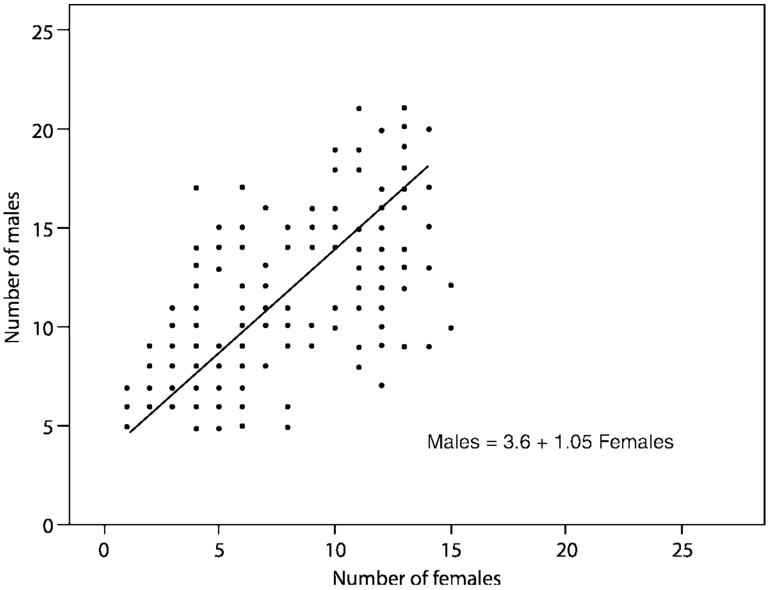

Fig. 4. The sex-ratio isodar of adult meadow voles occupying five different enclosures in the Lakehead University Habitron during summer 2008.

Male home ranges were larger and more plastic than those of females

Male home ranges were larger than female home ranges (males used ~0.35 'more' enclosures than did females; $t_{39} = 9.99$, $P < 0.001$). Mean home-range size contracted through time for both sexes. The contraction was far more rapid for males than for females (male home range = 2.72 – 0.016·day^{-1}, $F_{1,38} = 43.04$, $P < 0.001$, $R^2 = 0.53$; female home range = 2.10 – 0.005·day^{-1}, $F_{1,38} = 5.61$, $P = 0.02$, $R^2 = 0.13$; difference in home range size = 0.62 – 0.012·day^{-1}, $F_{1,38} = 27.03$, $P < 0.001$, $R^2 = 0.42$) (Fig. 5).

DISCUSSION

Theory and computer simulations document that differences in the reproductive interests of males and females create the potential for sexual conflict over habitat selection. The same theory demonstrates that sexual conflict can be revealed by a population's local sex-ratio isodar. Thus, the theory also documents that isodars, designed originally for studies of habitat selection (Morris, 1988), can solve numerous (and possibly all) density- and frequency-dependent evolutionary games.

Experiments on captive meadow voles, a species with clear reproductive conflicts between the sexes, confirmed the theory's predictions. The sex-ratio isodar was highly significant and local sex ratios of meadow voles were biased towards males despite a global sex-ratio of 1 : 1.

Our test of sexual conflict with meadow voles assumed that individuals were capable of assessing density-dependent differences between habitats in fitness, and that at least one sex can adjust its use of habitat away from the population's 1 : 1 sex ratio. To confirm these assumptions, we layered our design onto another verifying that individuals in this population of meadow voles select habitat in a density-dependent manner (Morris and

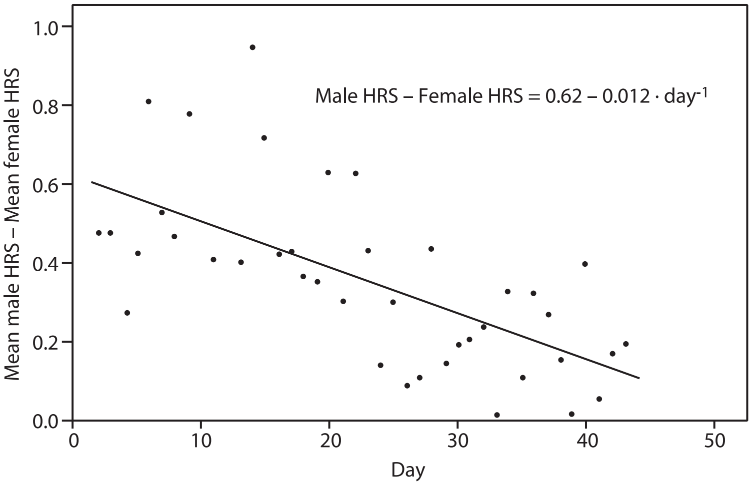

Fig. 5. The difference in mean home-range sizes (HRS) between adult male and female meadow voles declined through time (estimated as the difference between the mean number of enclosures in the Lakehead University Habitron used by males and the mean number used by females).

MacEachern, in press). When we added food to one enclosure, the voles congregated there. And, when we moved the food to a different enclosure, the voles followed. Vole densities thus responded positively to increases in resource supply, and negatively to reductions in food renewal. The combined experiments demonstrate that voles are active density-dependent habitat selectors, and that males and females are conflicted in their density-dependent habitat choices.

Our design was potentially compromised by the possibility that the number of males and females should tend towards equality at high population sizes (as might occur if the majority of marked animals used a single rich enclosure). Such an effect, when the isodar has a significant intercept as in our marked population of meadow voles, would bias the slope. Although we cannot exclude this possibility in our experiment, the isodar nevertheless clearly indicates sexual conflict over habitat selection. Despite a 1 : 1 population sex ratio, the sex-ratio isodar was strongly biased towards males at low densities, and maintained a constant number of 'surplus' males at all higher densities.

Sexual conflict over habitat selection in our population of marked meadow voles emerged because males maintained larger home ranges than did females. Home range sizes of both sexes declined through time, but home-range contraction was faster for males than for females. Home ranges of male meadow voles typically overlap those of many female territories as well as the home ranges of other males (Madison, 1980), presumably because it enhances mating opportunities (Madison, 1985; Wolff, 1985). There are at least two non-exclusive interpretations that can account for these multiple patterns. First, males may use their large home ranges to prospect for receptive females. If female territories contract because females converge on rich habitat, then male home ranges can contract even more and still overlap with numerous females. Second, female meadow voles may tolerate relatively more males at low densities so as to attain some minimum threshold of mate choice. If females tolerate relatively fewer suitors at higher densities, then male home ranges would contract through female aggression.

These alternatives demonstrate a richness of sexual conflict for habitat selection not yet addressed by theory. Asymmetries in reproductive effort between males and females, for example, suggest that females will cause density-dependent fitness to decline more quickly than will males, and that it will decline more rapidly still as the proportion of females in a habitat increases. Both effects will increase the potential for conflict that may manifest as sexual differences in habitat selection in a variety of otherwise confusing ways.

Sexual conflict over habitat may, for example, account for the observation that female Townsend's voles (*M. townsendii*) react more quickly to the addition of food than males (Taitt and Krebs, 1981, 1983). The same was true in experiments on prairie voles (*M. ochrogaster*) conducted by Lin and Batzli (2004). Although there was no response to supplemental food in identical experiments with *M. pennsylvanicus*, the settlement pattern of males differed from that of females (Lin and Batzli, 2004), a result consistent with sexual conflict over habitat. Movements of both *M. ochrogaster* and *M. pennsylvanicus* helped these species achieve ideal distributions of habitat use in which females were more abundant than males in food-supplemented habitats (Lin and Batzli, 2001). Lin and Batzli's results also confirm sexual conflict over habitat selection, as does habitat selection by reproducing female snow voles (*Clethrionomys nivalis*) that use different microhabitats than do males (Luque-Larena *et al.*, 2002). We can think of at least two potentially adaptive explanations for these consistent observations:

1. The extraordinarily expensive maternal reproductive costs associated with gestation and lactation by small mammals (Millar, 1977, 1978; Innes and Millar, 1981; Johnson *et al.*, 2001) are likely to yield a higher fitness premium from effective resource tracking by females than by males that provide no parental care. Female fitness in these species may be more tightly linked to resource availability (Boutin, 1990; Wauters and Lens, 1995; Koskela *et al.*, 1998; Koivula *et al.*, 2003) than is the fitness of males whose prospects are tied more closely with mating opportunities (recent examples include Perrin and Mazalov, 2000; Lehmann and Perrin, 2003; Lin and Batzli, 2004; Wild and Taylor, 2004). Thus, female habitat use could be expected to track resources, but with a time lag caused by a delay between changes in resource abundance and knowledge of that change. Male habitat use would simply track the changing distribution of females. This hypothesis could account for the more or less simultaneous departure of both sexes from enclosure 13 in our experiment, but it would appear incapable to account for the lack of a male response to supplemental feeding in enclosure 15.
2. Successful mating opportunities may require an abundance of males in species with multiple paternity such as meadow voles. If females maximize fitness by mating with (or choosing among) several males, then they may delay reproduction unless they have opportunity to mate with (or choose among) multiple suitors. Such a reproductive 'Allee effect' could force males to maintain larger home ranges than females, and to maintain relatively high use of habitats that are used by relatively few females.

Difficulty in resolving male habitat use is, however, consistent with sexual conflict over habitat selection. If the fitness functions for males and females are identical, then the number of males and females in a habitat would match perfectly. The linear sex-ratio isodar would pass through the origin with a slope of 1. But in our experiment, and despite equal numbers of each sex, males maintained a persistent, although variable (Fig. 4), numeric advantage over females (e.g. equation 8). The isodar thus strongly suggests that the fitness functions for males differ from those of females.

Maintaining large home ranges, and modifying their size differentially to that of females, may present an opportunity for male voles to minimize sexual conflict. Unable to adjust population sex ratios, they can nevertheless manipulate local sex ratios by altering home range size in response to female habitat selection. If female fitness is indeed more tightly linked to resource renewal than is male fitness, then males may be forced to match their spatial distribution to that of females. And if males track the distribution of females in some habitats, it may be necessary to avoid tracking females in other habitats in order to maximize fitness.

Behaviourally generated social conflict is likely to produce previously unanticipated interactions between the sexes. Whenever individuals of one sex alter their habitat selection to maximize fitness, individuals of the other sex may act to neutralize it through their own pattern of habitat selection. Contributions to fitness associated with resource density are likely to depart significantly between sexes in those species with asymmetric reproductive effort. We can thus expect, in such species, that sexual conflict for habitat will be revealed by the pattern of sex-ratio variation among habitats. Such appears to be the case for meadow voles where rapid changes in density occurred in response to differences in resource renewal while sex ratios fluctuated around a persistent male bias. These patterns further suggest that if one's interest is focused on population dynamics, then classical habitat isodars contrasting density between habitats are reliable indicators of relative habitat quality and its role in population growth. But if we wish to understand the evolutionary games played between the sexes, and more generally the struggle between cooperation and conflict, then we must add habitat selection to the list of traits and behaviours deserving our attention.

Regardless as to cause, and regardless of mechanisms that might minimize differences between sexes in habitat distribution, sexual conflict over habitat selection adds new dimensions to our understanding of habitat selection and the spatial strategies employed by males and females. Sex is, of course, but one binary metric of more general state-dependent differences among individuals. Our research demonstrates by theory, and experiment, that a full understanding of spatial (and likely temporal) distribution must consider differences in state as well as differences in density. It is equally apparent that a complete understanding of the respective roles of natural and sexual selection must also incorporate density-dependent differences in fitness and habitat choice.

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