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Female distribution affects mate searching and sexual selection in male northern water snakes (*Nerodia sipedon*)

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Abstract Mating systems and sexual selection are assumed to be affected by the distribution of critical resources. We use observations of 312 mating aggregations to compare mate-searching success of male northern water snakes (*Nerodia sipedon*) in two marshes in which differences in mating substrate availability resulted in more than fourfold differences in female dispersion. Reproductive males had significantly larger home ranges where females were dispersed than where females were clumped. The number of females encountered by males increased significantly with male home range size where females were dispersed, and decreased significantly where females were clumped. Where females were clumped, males were more likely to encounter other males when they located females. We found no evidence in either population that mate searching was energetically expensive or that males with relatively more energy had larger home ranges. However, males with greater fat reserves at the start of the season participated in more mating aggregations when females were dispersed, suggesting that fat reserves could affect a male's willingness to attempt mating or to persist in aggregations. When females were dispersed there was weak stabilizing selection acting to maintain male body size ($\beta=-0.14$), but strong directional selection favoring larger ($\beta=0.50$) and fatter ($\beta=0.37$) males. Over 7 years, the intensity of selection favoring larger males varied substantially ($\beta=0.14-1.15$), but that variation was not related to variation in the operational sex ratio. We found no evidence of directional selection on either body size ($\beta=0.05$) or fat reserves ($\beta=0.10$) of males when females were spatially clumped. Overall, the distribution of females had a

pronounced effect on male behavior, on the factors that affected male success in locating females, and probably on the extent of sperm competition once females had been located.

Key words Mate searching · Sexual dimorphism · Spatial patterns · Sexual selection · Northern water snakes · *Nerodia sipedon*

Introduction

For many animals, a male's reproductive success is limited by the number of females with which he can mate (Williams 1966; Trivers 1972). Thus, the spatial and temporal distributions of receptive females are key determinants of male reproductive strategies, and central to understanding mating systems (Emlen and Oring 1977; Arnold and Duvall 1994). If the spatial distribution of females varies in response to critical ecological resources, males are expected to respond by altering their own distribution (e.g., Ims 1988; Warner 1990; Brown and Brooks 1993). In turn, a change in the distribution of females and males is likely to affect the nature and intensity of sexual selection (Duvall et al. 1993). For example, if females are distributed unpredictably, males will have to search extensively for mates (Trivers 1972; Bondrup-Nielsen and Ims 1990; Duvall et al. 1993). Thus, any individual attribute that enhances male mate searching will be favored by selection (Ghiselin 1974). By contrast, when females are clumped in time and space, individual males may be able to monopolize multiple females, and thus the male traits that will be favored are those that aid in direct competition with other males. Here we examine the spatial predictability of receptive females and its effect on mate searching by males in northern water snakes (*Nerodia sipedon*). We take advantage of natural variation in female distribution in two study populations, and assess whether differences in male mate-searching behavior in the two populations alter the attributes that affect male success at obtaining mating opportunities.

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Northern water snakes are well suited to the spatial analysis we undertake here because their habitat during the active season is largely two-dimensional. Water snakes are highly aquatic (Scribner and Weatherhead 1995), spending nearly all their time either on the surface of the water or on substrate just above or beside the water. Mating begins following emergence and dispersal from hibernation in late April and early May, and continues until early June (Barry et al. 1992; Weatherhead et al. 1995). It occurs out of water on solid substrate and it is the distribution of this substrate that varied markedly between our two study sites (see below). Mating aggregations consist of a single female and often multiple males (Barry et al. 1992; Weatherhead et al. 1995). Both males and females regularly participate in more than one mating aggregation, and many females produce multiply sired litters (Barry et al. 1992). Within aggregations, males compete by insinuating themselves between the female and the other males. Males do not defend either mating sites or females against other males. Such scramble competition seems likely to place strong selection on males to find as many females as possible over a protracted breeding season. Schwagmeyer and Wootner (1986) found a similar pattern in thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), a mammal in which both sexes mate multiply and males are unable to control access to females through aggression.

Male snakes are often more active during the mating season (Madsen 1984; Gibbons and Semlitsch 1987; Reinert and Zappalorti 1988; Madsen et al. 1993; Aldridge and Brown 1995) and males may forego feeding during the mating season (King 1986). Male fat reserves may decrease dramatically over the breeding period, indicating that mate searching is energetically expensive (Bonnet and Nalleau 1996). Among water snakes, the fat reserves of small adult males are relatively larger than those of larger males (Weatherhead and Brown 1996). Thus, if mate-searching ability is limited by energy, selection should favor smaller males. Although it has been suggested that selection for enhanced mate-searching ability could favor small male size among snakes (Shine 1978, 1988; Weatherhead et al. 1995), only one study has addressed the question directly. Madsen et al. (1993) found that mate-searching ability was an important component of male reproductive success in European adders (*Vipera berus*), but mate-searching ability was not related to male body size. In previous research on water snakes, we found that in 1 of 4 study years, a male's stored energy was positively correlated with the number of aggregations in which he participated (Weatherhead et al. 1995; Weatherhead and Brown 1996). However, we did not consider how male mate-searching effort was affected by the spatial distribution of females or by variation in male size and energy reserves.

We compare male mate-searching behavior in two populations that differ substantially in the dispersion of reproductive females. We test four predictions. First, males should have larger home ranges during the mating season where females are dispersed than where females

are clumped. Second, in both populations, males with larger home ranges should encounter more receptive females, but the effect should be more pronounced where females are widely dispersed. Third, smaller males and males in better condition should have a greater mating advantage in the population where females are widely distributed. Thus, selection on male condition and small size should be stronger in the population in which males have to search more for mates. Finally, we had data for enough years from one marsh to assess how selection on males varied with the intensity of competition within the same marsh. We use the operational sex ratio (OSR; Emlen and Oring 1977) as our measure of competition, and test the prediction that any selection acting on males should be more intense as the OSR becomes more male biased.

Methods

General methods

We conducted this study at two marshes approximately 1 km apart, located 10 km from the Queen's University Biological Station in eastern Ontario, Canada (45°37' N, 76°13' W). Barbs Marsh and Beaver Marsh are 4 ha and 3 ha in area, respectively, with maximum depths <2 m. Barbs Marsh is spring fed, lacks permanent inflow or outflow channels, and is approximately 400 m from the nearest permanent water body. Beaver Marsh is also spring fed but is formed by beaver dams along the watercourse. Population genetic analysis indicates that these populations are relatively isolated, with very limited gene flow between them (Prosser et al. 1999). A key difference between the marshes relevant to this study is that at Beaver Marsh, the substrate (emergent vegetation, muskrat and beaver lodges) used by the snakes for mating occurs almost exclusively around the periphery of the marsh, the entire central part of the marsh being open water. By contrast, potential mating substrate occurs through much of Barbs Marsh, with less than 30% of the marsh as open water.

We captured snakes for marking and measuring either by hand or in minnow traps set along the shorelines of the marshes. We weighed snakes, measured their snout-vent length (SVL) and tail length, and marked them individually by branding caudal scutes or by subcutaneously inserting a passive integrated transponder tag (PIT tag; Anitech, Markham, Canada). We used the equation provided by Weatherhead and Brown (1996) to estimate the fat-free wet mass of each male from its SVL. We then subtracted this value from total wet mass to estimate an individual's fat mass. Fat mass was then divided by total mass to give relative fat content. To determine the energetic costs of mating activity, we calculated rates of mass change over the mating period for a sample of males captured and weighed both during the early part of the mating season and either late in the mating season or shortly thereafter.

Spatial patterns

We collected data on the spatial patterns of males, females, and mating aggregations in two ways. First, we used observations of marked individuals collected during the mating season from 1993 to 1996 at Barbs Marsh and from 1994 to 1996 at Beaver Marsh. We searched both marshes intensively for several hours at least once each day beginning in mid April before the snakes emerged from hibernation and continuing until mid June after all mating activity had ceased. Snakes captured during this period were individually marked with spots of non-toxic, acrylic paint, in addition to receiving PIT tags. Paint marks allowed us to identify snakes at a distance in the field without disturbing mating aggregations.

Most adults were measured and marked soon after emergence from hibernation, before the mating season began. By the latter half of the mating season, almost all individuals observed in aggregations were painted and could be identified. From 1993 to 1996, we observed only three unidentified males and five unidentified females in aggregations, or approximately 3% and 8%, respectively, of all snakes observed. Scale maps of both study sites were overlain with a 20×20 m grid. Each time we saw a paint-marked snake we recorded its grid location. Following the mating season we searched the marshes for snakes at least twice a week for the duration of the active season and recorded grid locations of all individuals captured.

We also used radio telemetry to monitor the activity of a sample of snakes throughout the active season, although here we report only on their activity during the mating season. Transmitters (Holohil Systems, Ottawa, Canada) were surgically implanted into the snakes' coelom. Transmitter mass was less than 7.5% of snake body mass. We tracked 20 females and 19 males for periods ranging from several months to 3 years. We located each individual with a transmitter at least once per day during the mating season.

We calculated home ranges for all snakes that we located a minimum of five times and in at least three different grid squares. We used a microcomputer software package (McPAAL, version 1.2, Smithsonian Institute, Front Royal, Va.) to construct and measure the area of snake home ranges, based on the coordinates of the center of each grid square in which they were located. The various methods for delimiting home ranges have their respective advantages and disadvantages (White and Garrot 1990). Because different home range protocols (e.g., minimum convex polygons, harmonic means; White and Garrot 1990) gave qualitatively similar results, we only report results obtained using the minimum-concave-polygon method. We used the midpoints of the reference grids in which we located snakes to estimate home ranges.

We estimated male success three ways. For most analyses we quantified male success as either the total number of mating aggregations in which each male was observed, or the total number of different females with which each male was observed in mating aggregations. However, we also recorded the number of other males seen in aggregations with each male. We analyzed these data separately to determine whether any individual attributes allowed some males to be more successful at locating unaccompanied females, or possibly discouraged other males from joining those males in aggregations.

To determine how variation in mating success could affect selection on male body size, we used multivariate analyses to calculate selection intensities (Lande and Arnold 1983). These analyses included data from males that were not observed in mating aggregations. We converted measures of mating success (number of aggregations and number of females) to relative scales by dividing the values for each individual by the mean values. These measures of relative fitness were then used as the dependent variable in multiple regressions with relative fat content, SVL, and a quadratic term for SVL [$SVL^2 = (SVL - \text{mean SVL})^2$; Endler 1986] as independent variables. In simple form, our model was:

$$\text{relative fitness} = \text{intercept} + \beta_1 \text{SVL} + \beta_2 \text{SVL}^2 + \beta_3 (\text{fat content})$$

where all independent variables have been standardized to a mean of 0 and standard deviation of 1 (Lande and Arnold 1983). The standardized coefficients from these multiple regressions (β_1 , β_2 , β_3) represent selection intensities on each trait after the effects of the other factors have been removed. β_1 and β_3 represent directional selection on SVL and fat content, respectively. A negative coefficient associated with the quadratic SVL term (β_2) indicates stabilizing selection acting on body size independent of relative fat content (which is negatively correlated with SVL and thus could also act to stabilize body size).

For males at Beaver Marsh, we pooled success data over the study period (1994–1996). For males at Barbs Marsh, we also pooled data over the study period (1993–1996), but only for success estimated by the number of different partners. For the number of mating aggregations in which males participated, we were able

to consider a longer period by combining data from this study (1994–1996) with earlier (1990–1993) data from Barbs Marsh reported previously (Weatherhead et al. 1995). Combining these data provided sufficient information for us to investigate annual variation in selection intensities and their relation to variation in the OSR. We calculated the OSR as the mean sex ratio of mating aggregations observed in each year. Some males were observed during the mating period in more than 1 year. Because male size and fat content changed between years, we treated data from the same male in different years as independent observations.

We considered males with a SVL of at least 42.5 cm and females with a SVL at least 55 cm to be sexually mature (Weatherhead et al. 1995). We restrict all analyses to sexually mature individuals in order not to confound lack of mating activity with sexual immaturity.

All analyses were performed using microcomputer versions of SAS (SAS 1987) and StatView (Abacus Concepts 1992). Significance was accepted at $P \leq 0.05$, although marginally non significant ($0.05 < P < 0.1$) results are discussed when deemed appropriate. We checked all tests for violation of assumptions and no transformations of data were required (Sokal and Rohlf 1981).

Results

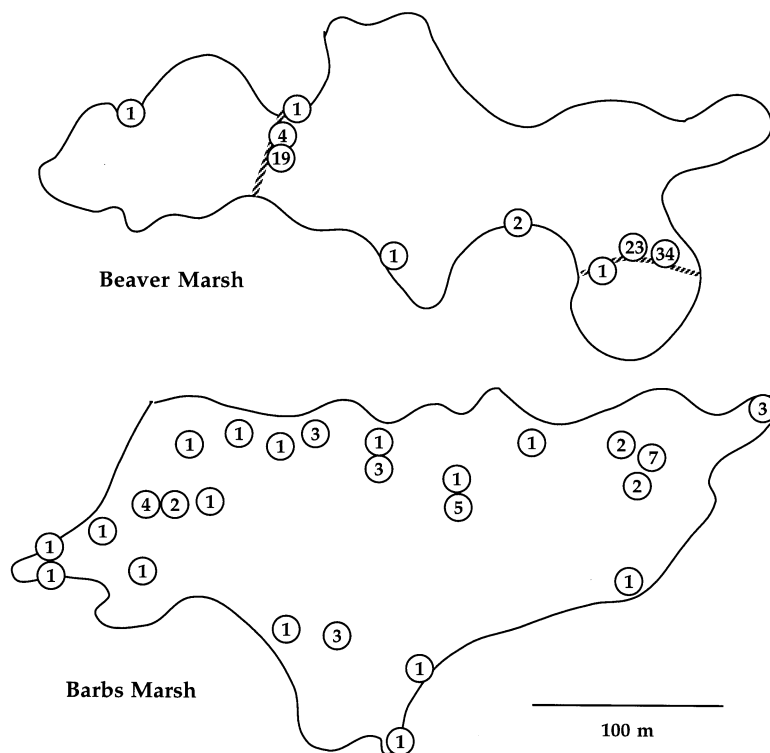
Distribution of mating aggregations

We observed 64 mating aggregations in Barbs Marsh between 1993 and 1996, 49 of which we mapped (unmapped aggregations were a consequence of incomplete location information from early in the study). At Beaver Marsh we observed 94 mating aggregations between 1994 and 1996, 86 of which we mapped. Consistent with our assumption that habitat differences between the two study marshes should result in different distributions of receptive females, mating aggregations were much more clumped at Beaver Marsh than at Barbs Marsh (Fig. 1). At Beaver Marsh most of the mating aggregations were located on the two beaver dams. The three grid squares with the most mating activity accounted for 88% of all aggregations in Beaver Marsh compared to only 33% of all aggregation in Barbs Marsh (Kolmogorov-Smirnov two-sample test, $P < 0.001$). Morista's index of dispersion (Krebs 1999) indicates that mating aggregations were more than four times more clumped in Beaver Marsh than in Barbs Marsh ($I_d = 20.4$ vs 4.6).

Home range size

During the mating seasons we observed 51 females and 66 males in Barbs Marsh and 30 females and 31 males in Beaver Marsh. Of these individuals, 39 were equipped with transmitters. Not surprisingly, we located transmitter-equipped snakes significantly more often than snakes without transmitters (mean number of sightings per individual: 21.7 vs 13.3, $t = 2.13$, $P < 0.0001$). Home range size increased with the number of times an individual was located ($r = 0.59$, $P < 0.0001$). Therefore, for analyses in which both groups of snakes were included, as our measure of home range size we used residuals from the regression of home range on the number of observations used to estimate home range.

Fig. 1 Maps of the study sites showing the locations of mating aggregations. Numbers in circles refer to the number of aggregations observed in that location. Beaver dams in Beaver Marsh indicated by heavy broken lines



Mean corrected home range areas for males were larger at Barbs Marsh than at Beaver Marsh (0.10 vs. -0.12 ha, $t_{79}=2.83$, $P=0.006$). This difference between marshes was attributable to reproductive males, because the difference was still apparent after excluding males never seen in aggregations (0.13 vs -0.12 ha, $t_{47}=2.44$, $P=0.018$). Among males never seen in aggregations, there was no difference in home range area between the two marshes (0.05 vs -0.10 ha, $t_{30}=0.15$, $P=0.16$).

At Barbs Marsh, there was no difference between the sexes in mean adjusted home range area when considering all individuals (0.004 vs 0.096 ha, $t_{97}=1.44$, $P=0.15$), or when analyses were restricted to individuals either seen in aggregations or not seen in aggregations (both $t < 1.43$, both $P > 0.16$). Similarly, at Beaver Marsh, there was no difference in mean home range area between males and females, either when all individuals were included in the analysis (-0.17 vs -0.12 ha, $t_{39}=1.29$, $P=0.20$), or when individuals were analyzed separately by mating status (both $t < 1.56$, both $P > 0.13$).

Home range size and mating

To assess how male home range size and activity related to their success at finding females, we first compared males known to have attempted mating (i.e., seen in at least one aggregation) with sexually mature males that were present during the mating season but not seen in a mating aggregation. We again used residuals from a regression of home range on the number of observations used to estimate home range size. At Barbs Marsh, males

Table 1 Comparison of mating season home range areas and number of sightings of reproductive and non-reproductive mature male *Nerodia sipedon*. Values are means \pm 1 SE followed by sample size in parentheses. Home ranges were estimated by minimum concave polygons. Residual areas are the residuals from a regression of home range area on the number of observations used to estimate home range. P -values are derived from t -tests comparing non-reproductive and reproductive snakes

	Non-reproductive	Reproductive	P
Barbs Marsh			
Sightings	6.87 \pm 1.13 (69)	14.32 \pm 1.37 (47)	0.0001
Area (ha)	0.29 \pm 0.08 (28)	0.53 \pm 0.07 (32)	0.28
Residual area (ha)	0.05 \pm 0.06 (289)	0.13 \pm 0.06 (32)	0.34
Beaver Marsh			
Sightings	4.04 \pm 0.84 (28)	6.88 \pm 0.58 (58)	0.007
Area (ha)	0.11 \pm 0.04 (4)	0.07 \pm 0.02 (17)	0.40
Residual area (ha)	-0.10 \pm 0.07 (4)	-0.12 \pm 0.03 (17)	0.78

seen in at least one mating aggregation were observed more often and had significantly larger home ranges than males not seen mating (Table 1). However, after correcting for the number of observations, the difference in home range size was not significant (Table 1). At Beaver Marsh, males seen mating were also seen more often than males not seen mating, but mean home range size did not differ between the two classes of males (Table 1).

It is possible that males not seen in mating aggregations did not attempt to mate, as opposed to simply having been unsuccessful at locating females. Thus, in our second approach to assessing how male mating success related to home range size, we considered only males

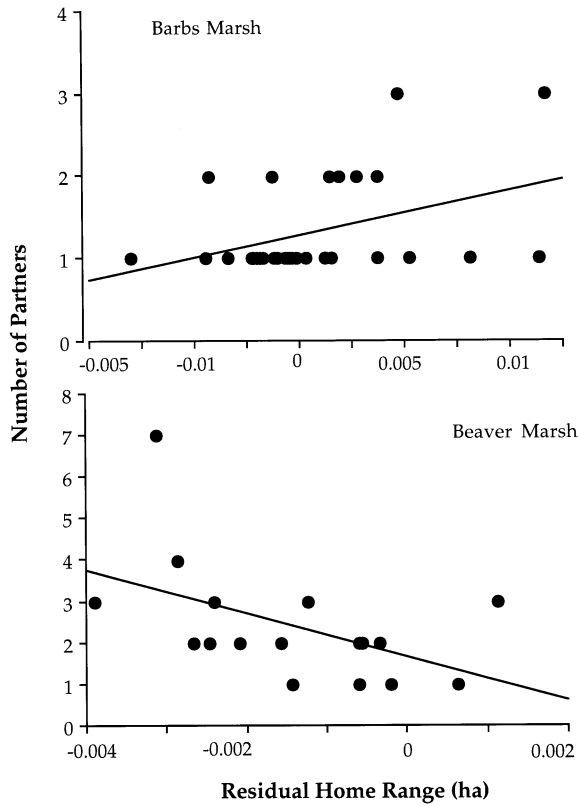


Fig. 2 Relationship between the number of different females a male was observed courting and the mating season home range size at Barbs and Beaver Marshes. Home range sizes are residuals from a regression of home range size on the number of observations used to calculate home range. Note the difference in scale for the two marshes to accommodate the larger home ranges in Barbs Marsh

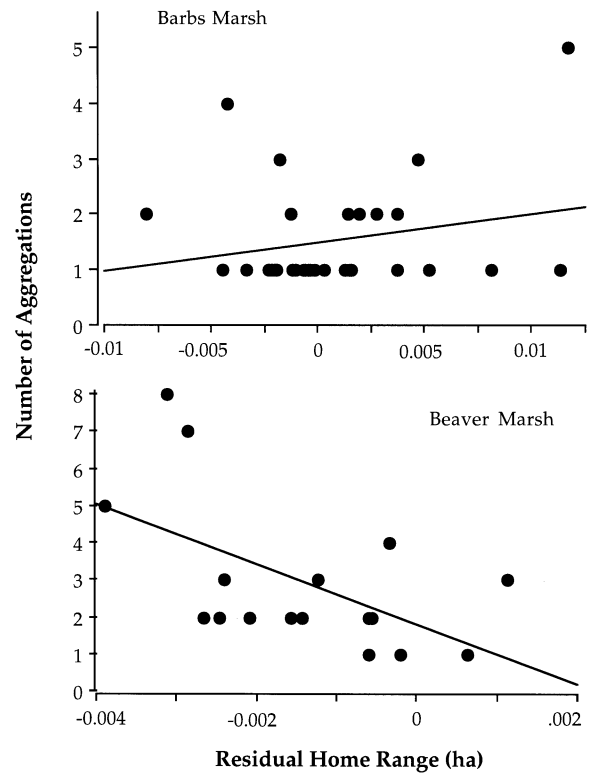


Fig. 3 Relationship between the number of mating aggregations in which a male was observed and mating season home range size at Barbs and Beaver Marsh. Home range sizes are residuals from a regression of home range size on the number of observations used to calculate home range. Note the difference in scale for the two marshes to accommodate the larger home ranges in Barbs Marsh

seen in at least one aggregation and thus known to have attempted to mate. Using the number of females as the dependent variable, and residual home range size and marsh as independent variables, there was a significant interaction between home range size and marsh ($F_{1,45}=13.25$, $P=0.0007$). The result was similar using number of aggregations as the measure of success (interaction $F_{1,45}=12.56$, $P=0.0009$). Thus, the relationship between home range size and mating success differed in the two marshes. Linear regression of success on residual home range size in the two marshes confirmed this. In Barbs Marsh, the number of females with which a male was seen increased significantly with home range size ($n=32$, $r=0.38$, $P=0.03$; Fig. 2), and the number of aggregations increased with home range size, although not significantly ($n=32$, $r=0.22$, $P=0.23$, Fig. 3). In Beaver Marsh, both measures of mating success decreased significantly with home range size (number of females: $n=17$, $r=-0.50$, $P=0.04$; aggregations: $r=-0.56$, $P=0.02$; Figs. 2, 3).

For a male to have a home range calculation, we must have seen him at least five times. We must also have seen him in at least three different grid squares that were not in a straight line, because we calculated home ranges as polygons using as points the center of each square in

which a male was observed. Thus, the estimated home range area of males observed in only one or two grid squares, or in three or more squares that were in a straight line would be 0. A consequence of our criteria for home range calculation is that relatively sedentary males were more likely to have been excluded from our analyses. This bias was useful in assessing whether males that attempted to mate were more sedentary when females were clumped than when dispersed. At Barbs Marsh, all 17 males that were seen in at least one aggregation but did not have home ranges calculated were excluded because they were seen fewer than five times (i.e., not because they were sedentary). By contrast, at Beaver Marsh, of the 34 reproductive males whose home ranges were not calculated, 21 were excluded because they were seen less than 5 times. Thirteen of these males were seen more than five times (up to 11 times) but we could not calculate home ranges for 8 of them because they were seen in only one or two grid squares. The remaining 5 males were excluded because they were seen in either three or four grid squares that were all in a straight line (i.e., along a beaver dam). Thus, spatial patterns for males that were excluded from the home range analysis also indicated that males were much more sedentary when females were clumped.

Male condition and mating

Home range area was not related to male size or relative fat content at either marsh (SVL: both $F < 1.34$, both $P > 0.31$; relative fat content: both $F < 1.06$, both $P > 0.31$). Thus, smaller males and males in better condition did not search larger areas during the mating season.

Mating activity did not appear to impose a heavy energetic cost on males. At Barbs Marsh, males that were never seen courting females lost mass at a mean rate of 0.06 g/day during the mating season, while males that were observed in aggregations gained mass at a rate of 0.004 g/day over the same period ($t = 0.58$, $df = 28$, $P = 0.57$). At Beaver Marsh, non-reproductive and reproductive males increased mass at rates of 0.17 g/day and 0.02 g/day, respectively ($t = 0.65$, $df = 27$, $P = 0.52$). At Barbs Marsh, the weight change of reproductive males over the mating season was not related to either SVL ($r = 0.34$, $n = 13$, $P = 0.26$), initial fat content ($r = -0.41$, $n = 13$, $P = 0.17$), or home range area (all $r^2 < 0.16$, all $P > 0.2$). Similarly, the weight change of males at Beaver Marsh was not related to SVL ($r = -0.33$, $n = 23$, $P = 0.13$), initial fat content ($r = 0.03$, $n = 23$, $P = 0.91$) or home range area (all $r^2 < 0.32$, all $P > 0.09$).

Male attributes and intrasexual competition

To determine whether male phenotype or home range size affected intrasexual competition, we considered all males seen in at least one aggregation. We classified them as either never having been observed in an aggregation with other males, or as having been observed in an aggregation with at least one other male. At Barbs Marsh, males seen alone with females ($n = 27$) and those seen competing with other males ($n = 16$) did not differ in mean SVL (53.4 vs 54.4 cm, $t = 0.58$, $P = 0.56$) or mean percentage fat (0.16 vs 0.19, $t = 1.30$, $P = 0.20$). For males for which we could calculate home ranges, males seen alone ($n = 19$) and those seen with other males ($n = 9$) had similar-sized home ranges (0.4 vs 0.6 ha, $t = 0.90$, $P = 0.39$). At Beaver Marsh, there were also no differences between males seen alone ($n = 22$) and those seen with other males ($n = 30$) in mean SVL (52.6 vs 52.6 cm, $t = 0.03$, $P = 0.98$) and mean percentage fat (0.19 vs 0.19, $t = 0.20$, $P = 0.84$), or in mean home range area ($n = 4$ and 11, respectively, means = 0.04 vs 0.09 ha, $t = 1.60$, $P = 0.14$).

The preceding analyses indicate that body size, fat content, and home range size did not affect the competition males faced for access to females. However, one pattern that did emerge was that the distribution of females appeared to affect male competition. At Barbs Marsh, where females were relatively dispersed, 63% (27/43) of aggregations involved one male, while at Beaver Marsh, where females were more clustered, 42% of aggregations involved a single male (Fisher's exact test, $P = 0.06$). Thus, males successful at locating females at Beaver Marsh were somewhat more likely to have to compete with other males for access to those females.

Table 2 Intensities of directional selection on body size and relative fat content (β_1 , β_3) and stabilizing selection on snout-vent length (SVL) (β_2) of male *N. sipedon*, based on the number of mating aggregations in which a male was observed and the number of different females he courted

	<i>n</i>	Number of years	SVL		Fat content
			β_1	β_2	β_3
Barbs Marsh					
Aggregations	225	7	0.502***	-0.139	0.370***
Partners	118	4	0.485***	-0.199	0.224
Beaver Marsh					
Aggregations	87	3	0.054	-0.035	0.099
Partners	87	3	0.094	-0.015	0.129

*** $P < 0.001$

Selection intensity

Calculations of selection intensities include data from males that were sexually mature but were not observed in mating aggregations. Thus, these analyses do not distinguish between males that did not attempt to mate and males that were simply unsuccessful at locating receptive females. The intensities of directional and stabilizing selection acting on SVL and directional selection on relative fat content were weak and non-significant at Beaver Marsh for both methods of estimating male success (Table 2). At Barbs Marsh, there was strong directional selection on SVL (favoring larger males) for both estimates of success (Table 2). There was also moderate but non-significant stabilizing selection on SVL, indicated by the negative values of β_2 . When we used the number of mating aggregations as the index of male success, there was strong directional selection on relative fat content (Table 2). This selection is weaker when number of different females is used to estimate male success (Table 2). Thus, there are notable differences between the two sites in the intensity of selection acting on male body size. Although there was evidence of stabilizing selection acting on body size at each site, the magnitude of directional selection acting to increase body size was greater when females were more dispersed. After controlling for body size effects, there was directional selection of varying magnitude acting to increase relative fat content. Despite differences between sites in the intensity of selection on body size, there was no difference between sites in the body size of adult males in the two marshes ($n = 117$ and 87 for Barbs and Beaver, respectively; $t = 1.00$, $P = 0.32$). Interestingly, males from Beaver were significantly fatter than males from Barbs ($t = 2.11$, $P = 0.04$), despite stronger selection on fat content for males in Barbs. This difference may result from greater use of their fat reserves by the males in Barbs Marsh.

Using the number of aggregations in which males participated as the measure of male success, we calculated annual selection intensities over 7 consecutive years at Barbs Marsh (Table 3). The intensity of selection acting on body size and relative fat content varied by an or-

Table 3 Intensities of directional selection on body size and relative fat content (β_1 , β_3) and stabilizing selection on SVL (β_2) of male *N. sipedon* in Barbs Marsh over 7 years, in relation to the operational sex ratio (OSR). Selection intensities were calculated using the number of mating aggregations in which each male was observed as an estimate of reproductive success. n is the number of males

Year	n	SVL		Relative Fat	OSR
		β_1	β_2	β_3	
1990	40	0.45**	-0.04	0.43**	0.36
1991	34	0.14	-0.26	-0.21	0.43
1992	33	0.64*	-0.09	0.10	0.57
1993	33	0.93**	-0.36	0.40	0.74
1994	33	0.14	-0.29	0.02	0.77
1995	25	1.15**	0.14	0.31	0.75
1996	27	0.29	-0.35	0.12	0.83

* $P < 0.05$; ** $P < 0.01$

der of magnitude among years. However, this annual variation was unrelated to variation in the OSR (both $F < 0.46$, both $P > 0.53$).

Discussion

Understanding how sexual selection operates and its consequences for a particular species ultimately requires understanding the ecological factors that underlie competition for mates in that species (Emlen and Oring 1977; Andersson 1994). It logically follows from this premise that one must also understand how those ecological factors vary among populations of the species, lest the serendipitous choice of a study population determine the outcome of one's study. At two study sites only a kilometer apart, we found that competition among male water snakes for access to females varied substantially, largely as a consequence of the spatial distribution of substrate appropriate for mating. Females were more than four times more clumped at one site than the other, which affected male mate-searching behavior and the factors that affected male success at locating females.

Males appeared to adjust their home ranges to reflect the distribution of females during the mating season. At Beaver Marsh, where receptive females were found mostly on beaver dams, males restricted their activity to small home ranges. By contrast, at Barbs Marsh, males had much larger home ranges. The number of females encountered by males increased with the size of their home ranges at Barbs Marsh, while at Beaver Marsh, males with larger home ranges actually encountered fewer females. The positive relationship between home range size and mating opportunity at Barbs Marsh is similar to that found by Madsen et al. (1993) in adders. They found that males that moved greater distances during the breeding season obtained more matings. Thus, when receptive females are widely or unpredictably distributed, mate-searching activity appears to be an important component of reproductive success for male snakes. The negative relationship between mating and home range size at Beaver Marsh suggests that

males that did not restrict their activity to the areas where females were found forfeited breeding opportunities.

When larger home ranges increase male mating opportunities, the contributory factors should be subject to sexual selection. Madsen et al. (1993) found no relationship between the distances moved by male adders and their body size. Similarly, we found that home range areas of male water snakes were unrelated to either their body size or energy reserves. Failure to find a relationship between home range area and energy reserves was unexpected, given that movement requires energy and that previous studies had indicated that male water snakes forego feeding during the mating season and steadily lose weight (Feaver 1977; King 1986). However, males in our study populations readily fed during the mating season and were often captured in minnow traps (presumably while foraging). It is possible that males searching for mates may opportunistically encounter and capture prey without greatly diminishing their effectiveness at finding females.

A major objective of our research is to understand how sexual selection on males contributes to sexual size dimorphism in *N. sipedon* in which males are the smaller sex (Weatherhead et al. 1995; Brown and Weatherhead 1999). Although male size did not explain variation in male home range size, mating activity varied with male size and fat reserves, but differently in the two marshes. Both larger body size and greater relative fat reserves increased male mating opportunities at Barbs Marsh, while at Beaver Marsh, variation in male mating success was unrelated to body size or fat reserves. The positive influence of fat reserves on male mating opportunities in Barbs Marsh is interesting given that fat reserves were not related to home range size. It is possible that a male's fat reserves influenced whether he attempted to mate in a given year, and if he did attempt to mate, his willingness to persist in aggregations, rather than affecting his ability to find females.

Selection intensities revealed clear evidence of selection on both the size and fat reserves of males in Barbs Marsh. Directional selection favoring large males appeared to be acting simultaneously with weak stabilizing selection limiting male size. Thus, beyond some optimal size, male success decreased. The reason for this is unknown, but it is independent of both the decrease in relative fat content associated with increased male size (Weatherhead and Brown 1996), and also of mate searching ability. Given the relative weakness of stabilizing selection on male body size, sexual selection acting through male success locating females appears not to play a major role in maintaining the small size of males relative to females. Selection intensities in Beaver Marsh were much weaker than in Barbs Marsh. However, one indication that there may have been some similarity in the factors that affected male mating success in the two marshes was that the sign of the selection intensities was the same in both marshes.

Annual variation in selection over 7 years in Barbs Marsh was not related to variation in the OSR. This was contrary to evidence from other species that a skew in the OSR affects the intensity and outcome of competi-

tion among males (e.g., Hoglund 1989; Madsen and Shine 1993). However, male water snakes engage in scramble competition rather than defending females. Thus, at least to the point that we measured male success (i.e., locating receptive females), variation in the relative number of males competing for females has limited potential for affecting male success.

Males must find and court females to have some prospect of reproductive success. However, copulation, insemination, and fertilization are all necessary to complete the process. We do not yet know how mating opportunities translate into reproductive success for male water snakes. However, we do know that the spatial distribution of a simple ecological variable (mating substrate) exerts a strong influence on sexual selection on males up to the point that females are located. Furthermore, the distribution of females also affected the likelihood that receptive females were located by more than one male simultaneously and, thus, the potential for multiple mating and sperm competition. Determining the factors that affect male success once females have been located should provide the opportunity to understand the link between ecology and sexual selection in water snakes.

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