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## Effects of reproduction on the antipredator tactics of snakes (*Tropidonophis mairii*, Colubridae)

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**Abstract** Does an animal's reproductive state influence the distance at which it flees from an approaching predator? We predicted that reproduction would increase approach distances in pregnant females (because they are burdened with eggs and thus less able to escape rapidly), but reduce them in males (because of lower vigilance due to males focusing on mate-searching rather than predator detection). Field data on approach distances of keelback snakes (*Tropidonophis mairii*, Natricinae, Colubridae) supported both of these predictions. We walked the same 1.3-km transect along a dam wall in tropical Australia on 135 nights, and recorded the distances at which snakes fled from our approach. Locomotor speeds were measured for a subset of these animals. Variations in approach distance due to season, weather conditions, prior capture history and snake body size were minor, but reproduction strongly affected approach distances for snakes of both sexes. Gravid females were slower than non-gravid females, and fled at greater distances. Reproductive status did not affect locomotor speeds of males, but males that were reproductive (i.e., contained sperm) permitted closer approach than did non-reproductive adult males. Reproduction thus affected approach distances in snakes of both sexes, but in opposite directions and for different reasons.

**Keywords** Approach distance · Cost of reproduction · Locomotor ability · Reptile

### Introduction

Predation is a significant source of mortality for many species of animals, and has acted as a potent selective

force on a diverse array of morphological and behavioral traits (e.g., Vermeij 1982; Endler 1986). An animal faced with an approaching predator must make a series of “decisions” as to which antipredator tactics (e.g., crypsis, flight, display) to adopt, and how closely the predator should be allowed to approach before those tactics are implemented. Thus, one of the most important antipredator decisions concerns approach distance (Lima and Dill 1990; Magnhagen 1991). Fleeing when the predator is so far away that it poses no real threat entails costs in wasted time and energy, whereas delaying flight for too long can increase the animal's vulnerability if the predator does indeed launch an attack. Optimality models thus suggest that animals should adjust approach distances relative to their own locomotor abilities: a faster animal can safely allow closer approach (Lima and Dill 1990; Dickman et al. 1991). Similarly, approach distances may vary if some individuals are engaged in activities (e.g., social interactions, mate searching) that decrease antipredator vigilance.

Studies on reptiles provide empirical support for this prediction. For example, increased body temperatures (and thus locomotor speeds) decrease approach distances in lizards (e.g., Smith 1997; Cooper 2000). Some of the most dramatic temporal shifts in antipredator tactics relate to reproductive activities. Although reproduction may influence antipredator tactics in both sexes, the causal pathways appear to differ. In squamate (snake and lizard) species, in which gravid (pregnant) females are slowed-down by the burden of the clutch (Shine 1980; Seigel et al. 1987), such animals tend to reduce foraging activities and remain close to cover (Bauwens and Thoen 1981; Brodie 1989; Schwarzkopf and Shine 1992). This shift has been interpreted as an adaptive response to the lowered mobility (and hence, predator-escape ability) of such heavily burdened females. In contrast, a shift in the antipredator behavior of male snakes during the reproductive season, as evidenced by high mortality rates at this time, has been attributed to a much simpler and more direct mechanism: that reproductive males focus on mate-

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searching rather than predator evasion (Shine 1994; Alldridge and Brown 1995; Bonnet et al. 1999).

We might thus expect that reproduction would modify antipredator responses of both sexes, but in opposite directions and via different pathways. Specifically, we predict that: (1) approach distances will be greater for reproductive than for non-reproductive female snakes, as an adaptive response to their decreased mobility due to pregnancy; and (2) approach distances will be smaller for reproductive than for non-reproductive males, because the former group are focused on mate-searching and thus are less vigilant.

Our long-term field studies on snakes in tropical Australia provided an ideal opportunity to collect information on this topic. During nightly trips to collect snakes as part of a mark-recapture program, we recorded the approach distance of each snake that we captured. We also measured locomotor speeds of a subset of these animals, to examine the assumption that reproductive state would influence mobility in females but not males. We can thus evaluate the way in which reproductive and non-reproductive individuals within each sex responded to our approach, as well as to examine the complicating effects of other factors such as locomotor speed, body size, previous capture history and season on antipredator behavior.

## Methods

### Study area

We collected snakes along the wall of Fogg Dam, an artificial impoundment on the Adelaide River floodplain 60 km SE of Darwin in the Northern Territory. The dam wall is 1.3-km long and approximately 10-m wide, with standing water to the south of the wall. The floodplain north of the dam wall is inundated for a few months during the wet-season, but is dry for the rest of the year. Further details on climatic features and topography have been provided elsewhere (Madsen and Shine 1998).

### Study species

Keelbacks (*Tropidonophis mairii*) are non-venomous natricine colubrid snakes widely distributed across tropical and subtropical coastal habitats in Australia (Cogger 2000). In our study area, adult females (mean snout-vent length 55.5 cm, mean mass 100 g) grow larger than males (mean SVL 47.5 cm, mean mass 56 g). Female keelbacks also mature at a larger body size (45 cm SVL, based on the presence of oviductal eggs) than do males (30 cm SVL, based on the presence of sperm in cloacal smears). Females produce multiple clutches of 4–18 eggs between May and November, during the dry-season (Brown and Shine 2002). Oviposition cycles are non-synchronous among females, so that it is possible to find both reproductive and non-reproductive individuals in the same area at the same time. Most adult males captured throughout the year contain sperm. However, up to 15% of adult males captured each month do not contain sperm (Brown and Shine, unpublished data), again facilitating comparison between reproductive and non-reproductive animals encountered at the same time. We do not know whether adult-sized males without sperm have temporarily ceased production of sperm or whether they have depleted their stores of sperm. In either case, they are unlikely to be engaged in mate-searching activity as intensively as are males containing sperm. Males sometimes switch between reproductive states from one

capture to the next, and reproductive and non-reproductive males do not differ in body condition or recapture probability (Brown and Shine, unpublished data). However, reproductive males and males that switched status grew more slowly than did nonreproductive males, suggesting an energetic cost associated with containing sperm (unpublished data). Keelbacks feed primarily upon frogs, and are crepuscular and nocturnal in habits (Shine 1991). They are presumably killed and eaten by a wide range of predators, including wading birds, raptors, varanid lizards and other snake species, but there are no quantitative data on this topic.

### Methods

We walked along the dam wall for an average of 76 min each night, beginning at dusk (approx. 1900 hours). Data for the present paper were gathered on 135 nights over the period 7 April 2001 to 25 May 2003. Snakes were located with a flashlight, generally from a distance of >3 m. Only snakes with their heads visible (i.e., that could see our approach) were used for antipredator trials. All snakes were approached directly, at a quick walking pace (approx. 2 m/s), and we recorded the distance from us at which the snake fled. We recorded approach distances as number of paces away from the snake when it first began to move (approximately 1 m per pace, or if it was within arms' length as 0.5 m). In 136 of 254 cases, the snake remained stationary until it was seized. None of the snakes approached for antipredator trials escaped.

All captured snakes were returned to the field laboratory for processing and marking, before being released at their capture sites the following evening (except for gravid females, which were retained until oviposition). We recorded snout-vent length, mass, sex and reproductive status. Gravid females were immediately recognizable by their distended bodies, and this was confirmed in every case by palpation of oviductal eggs (and subsequent oviposition). Status of nonreproductive females was also confirmed by palpation. To characterize reproductive state of each male, a thumb was gently run posteriorly along the snake's ventral surface several times and the hemipenes were everted and touched to a drop of water on a microscope slide. The hemipenes were then retracted and the base of the tail was gently massaged. The hemipenes were everted again and gently smeared along the slide. The slide was then examined for the presence of spermatozoa under 100 $\times$  power. Males from which sperm were obtained were classed as reproductive. If no sperm was evident on a slide obtained from a male, the process was repeated a second time. If sperm were absent from both slides, the male was classed as non-reproductive. To assess the accuracy of this method we took a third smear from 23 nonreproductive males. There were no cases where sperm was present on a third smear if it was absent from the first two.

Climatic data (air temperature, relative humidity) were recorded on most evenings between 7 April 2001 and 24 April 2003 at Middle Point Village approximately 1.5 km from Fogg Dam. Data on moonlight (proportion of the moon illuminated) at our study site each evening during this period were taken from the website <http://aa.usno.navy.mil/AA/data>. Temperatures ranged from 20.5 $^{\circ}$ C to 29.6 $^{\circ}$ C (mean 27.1 $^{\circ}$ C), relative humidity ranged from 43.5% to 100.0% (mean 81.0%) and moon illumination ranged from 0 to 100% (mean 34%).

### Locomotor performance

To determine the extent to which reproductive condition affected sprint speed of keelbacks, we measured the time it took individuals to crawl 5 m. To maximize relevance to the field situation, these trials were conducted outdoors in a 6-m metal trough filled to a depth of 5 cm with gravel. Trials were conducted at night and snakes fled from the same stimulus used for the field encounters (i.e., an investigator walking towards them wearing a head lamp as they crawled down the raceway).

## Ethical note

Research was conducted under Scientific Licence no. 13627 from the Parks and Wildlife Commission of the Northern Territory, and Animal Care and Ethics Approval L04/7–2001/3/3411 from the University of Sydney. All snakes were collected by hand and transported to the laboratory in clean cloth bags. Snakes were individually marked by clipping the edges of up to four ventral scales, with no apparent adverse effects. Hundreds of these animals have been recaptured over many years with no signs of trauma or infection at the scale clips. Female snakes retained until oviposition were kept singly in 40×30×21 cm plastic containers, lined with newspaper and housed indoors. Each cage had a water bowl and a container of damp vermiculite for oviposition. Gravid females do not eat in the wild (personal observation) so they were not fed during the time (maximum of 10 days) they were held under these conditions. The females were released immediately after oviposition, at their original capture site. Their eggs were incubated in the laboratory and hatchlings were marked by clipping ventral scales (as above) and then released. Many of these marked offspring also have been recaptured, with no difference in recapture rates among babies with 2, 3 or 4 clipped scales (unpublished data).

## Analyses

We used ANOVA to determine the effects of categorical variables on approach distance. We used simple linear or multiple regression to determine the effect of continuous variables. Significance was accepted at  $\alpha = 0.05$ . Analyses were conducted using the software programs JMP (SAS Institute 2002) and Statview 5 (SAS Institute 1998).

## Results

### Antipredator response

We encountered 628 keelbacks over the 135 nights, and captured 553 of them. Antipredator data were taken for 284 of these captures. Most of the remaining snakes could not be approached in a standardized manner because their heads were completely or partly concealed by vegetation or because they were moving when first seen. Of the 284 keelbacks for which we scored antipredator responses (1 juvenile male, 33 juvenile females, 132 adult males, 118 adult females), 199 allowed us to approach to  $\leq 0.5$  m (70%) whereas the other 85 (30%) fled at greater distances.

Fifty-eight of the 284 snakes had been captured previously. The mean time elapsed since the last capture was 229 days (range 7–1,008 days). The mean number of times the snakes had been captured previously was 1.22 (range 1–3 previous captures). There was no difference in approach distance between snakes that had been captured previously and naive, newly encountered snakes (Table 1). Among snakes that had been captured previously, there was no effect of time since last capture ( $F_{1,56}=1.25$ ,  $P=0.27$ ). Snakes that had been captured more often allowed closer approach, though not significantly ( $F_{1,56}=3.47$ ,  $P=0.07$ ).

One-way ANOVAs investigating the effects of categorical variables on approach distance revealed no effects of sex (male vs female), reproductive condition (reproductive vs not reproductive), age (adult vs juvenile), pre-

**Table 1** Summary of univariate analyses of factors affecting antipredator response of keelback snakes, (*Tropidonophis mairii*). Mean approach distances (m) are given for categorical independent variables and slopes from linear regressions are given for continuous independent variables. Values in parentheses are standard errors

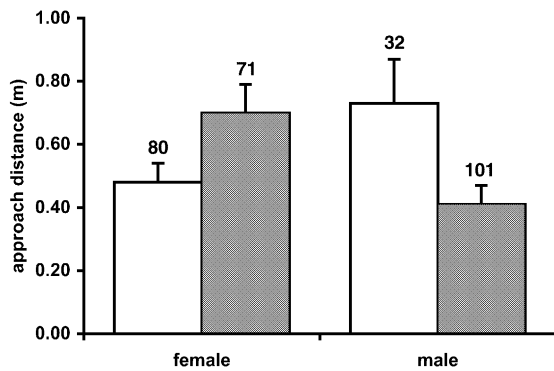
Independent variable	Category	<i>n</i>	Mean approach distance or slope	<i>F</i>	<i>P</i>
Age	Juvenile	34	0.41 (0.08)	1.41	0.24
	Adult	250	0.56 (0.04)		
Sex	Male	133	0.49 (0.06)	1.48	0.23
	Female	151	0.59 (0.06)		
Reproductive status	Reproductive	172	0.53 (0.05)	0.07	0.79
	Nonreproductive	112	0.55 (0.06)		
Recapture status	New	226	0.54 (0.04)	0.001	0.97
	Recapture	58	0.54 (0.10)		
Month	Apr	112	0.47 (0.06)	1.29	0.27
	May	96	0.68 (0.08)		
	Jun	26	0.50 (0.12)		
	Jul-Sep	20	0.45 (0.15)		
	Oct-Nov	17	0.38 (0.16)		
	Dec-Jan	13	0.54 (0.16)		
Body size		284	0.005 (0.005)	1.24	0.27
Air temperature		172	-0.01 (0.03)	0.25	0.62
Relative humidity		172	0.002 (0.005)	0.20	0.66
Moonlight		240	-0.14 (0.10)	2.16	0.14

**Table 2** Two-way ANOVA results of the effects of sex and reproductive status (reproductive vs nonreproductive) on approach distances of keelback snakes

Source	<i>df</i>	<i>F</i>	<i>P</i>
Sex	1	0.05	0.82
Reproductive status	1	0.33	0.56
Sex × reproductive status	1	9.98	0.0018

vious capture history (new capture vs recapture) or month (Table 1). Linear regressions indicated that approach distances were not affected by body size, air temperature, relative humidity or amount of moonlight (Table 1).

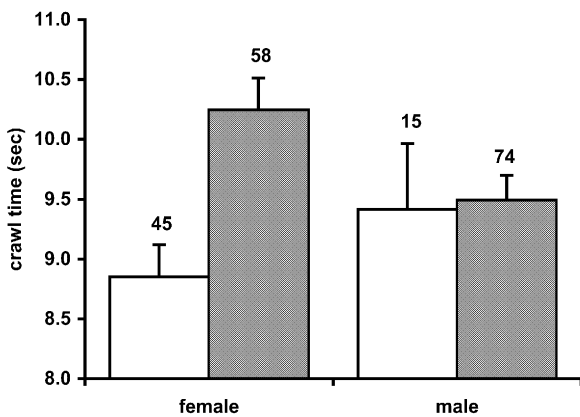
However, inspection of our data suggested that effects of reproductive condition on approach distance differed between males and females. A two-factor ANOVA revealed a significant interaction between sex and reproductive status (Table 2, Fig. 1). This effect remained significant even after including further individual characteristics (recapture status, body size) into the model (Table 3). The significant interaction term reflected opposing trends in the two sexes: reproductive males permitted closer approach than did non-reproductive males, but the reverse was true in females (Fig. 1). The magnitude of the effect of reproduction on approach distances was similar in males and females (-45% vs +45% changes respectively) and was statistically significant in each case (males,  $F_{1,131}=5.98$ ,  $P=0.016$ ; females,  $F_{1,149}=4.10$ ,  $P=0.044$ ).



**Fig. 1** Mean approach distances of keelback snakes (*Tropidonophis mairii*). Filled bars indicate reproductive individuals (based on the presence of eggs or sperm), unfilled bars represent non-reproductive individuals. Error bars indicate standard errors, numbers above bars indicate sample sizes

**Table 3** Multiple regression model results of factors affecting the approach distance of keelback snakes

Source	df	F	P
Capture history	1	0.07	0.80
Snout-vent length	1	0.37	0.55
Sex	1	0.00	0.99
Reproductive status	1	0.63	0.43
Sex × reproductive status	1	9.39	0.0024



**Fig. 2** Time taken to crawl 5 m by male and female keelbacks. Filled bars indicate reproductive individuals and open bars indicate nonreproductive individuals. Error bars represent standard errors, numbers above bars indicate sample sizes

### Locomotor performance

Locomotor trials were carried out on 58 reproductive females, 45 non-reproductive females, 74 reproductive males and 15 non-reproductive males. A two-factor ANOVA with sex and reproductive condition as independent variables revealed a significant interaction ( $F_{1,184}=4.08$ ,  $P=0.045$ ; Fig. 2): that is, reproduction affected locomotor speed differently in males and females. Among females, reproductive individuals took

significantly longer to crawl the 5-m distance than did non-reproductive individuals (10.2 s (SD=2.0) vs 8.9 s (SD=1.8), unpaired  $t_{98}=13.05$ ,  $P=0.0005$ ). In contrast, reproductive status did not affect the locomotor ability of males (9.5 s (SD=1.8) vs 9.4 s (SD=2.1), unpaired  $t$ -test:  $t_{86}=0.15$ ,  $P=0.89$ ).

### Discussion

Does the distance at which free-ranging snakes fled from our approach offer a useful index of antipredator tactics, despite the artificial nature of the stimulus? We have no information on the validity of this important assumption, but detailed studies on other natricine snakes have revealed that the animals respond to the approach of humans in a similar way as they do to more natural predatory stimuli (Scudder and Chiszar 1977; Herzog et al. 1989; Shine et al. 2000). Indeed, most natricine snakes retreat rapidly from any novel and potentially threatening stimulus (personal observation).

Even if approach by a human (as used in the present study) does not closely mimic a natural predator attack, it is an appropriate stimulus to test whether snakes captured once are more difficult to recapture (see also Labra and Leonard 1999). Our results indicate that snakes did not become more wary after they had been captured once, nor did they become more wary if they had been caught more recently or more often. It is an important assumption of mark-recapture methodology that the act of capturing, handling and marking an individual does not affect its likelihood of being captured again, though this is rarely tested directly (Murray and Fuller 2000). In the case of keelbacks, the experience of being captured did not subsequently cause the snakes to become more vigilant or more ready to flee from an approaching human. Indeed, snakes that had been captured more often were slightly less likely to flee from an approaching human during subsequent encounters.

Similarly, approach distances were unaffected by abiotic variables (temperature, humidity, moonlight) or by snake body sizes (Table 1). Such variables have been implicated as major determinants of antipredator responses in previous studies on reptiles (e.g., Martin and Lopez 1995; Cooper 1997, 2000; Passek and Gillingham 1997; Smith 1997; Whitaker and Shine 1999; Shine et al. 2002). Why did these factors fail to affect keelback approach distances? The likely answer is that the most consistent such effect in previous studies involves temperature, and previous studies generally have included individuals that were tested over a very wide range of temperatures, wide enough, for example, to significantly affect locomotor speeds. In turn, this range of temperatures was included because the studies were either performed in the laboratory, or on free-ranging animals in temperate-zone climates where the diel range of body temperatures is high. For example, a desert lizard basking soon after morning emergence will be much colder (and thus may show a different approach distance) than the same lizard en-



countered a few hours later at midday. In contrast, temperatures are high year-round in the tropical environment of our study area, and thus shortly after dusk when keelbacks are active (Shine 1991) they experience a relatively small range of ambient temperatures (Brown and Shine, unpublished data). Hence, the abiotic conditions tested were all within the range in which the snakes' performance (e.g., locomotor, sensory) was at similar (and perhaps close to optimal) levels. The lack of significant abiotic effects on approach distances in the present study facilitates investigation of other effects. In some circumstances, abiotic factors may not affect antipredator tactics even in temperate-zone animals; for example, approach distances for basking northern water snakes (*Nerodia sipedon*) were unaffected by the temperature of the water into which the snakes escaped (Weatherhead and Robertson 1992).

Reproduction affected the antipredator responses of keelbacks of both sexes, but did so differently in males and females. Males that were reproductively active (i.e., contained sperm) tolerated closer approach than did non-reproductive animals. In contrast, females that were reproductive (i.e., contained eggs) fled from our approach at a greater distance than did non-gravid animals. These effects cannot be attributed to other differences between reproductive and non-reproductive animals, because plausible candidates for such confounding traits (e.g., body size, season, weather conditions at the time) either did not differ between reproductive and non-reproductive animals or did not influence antipredator responses (see above). Analyses that included all of these factors (and hence, took their effects into account) thus strongly suggest that reproductive status influenced antipredator responses in keelbacks, albeit in opposite directions in the two sexes.

The likely reason why reproductive male keelbacks tolerated our close approach is simply that they were less vigilant than were non-reproductive animals (see also Cooper 1997). Reproductive males are notoriously single-minded in many animal species, including snakes (Shine et al. 2001). Several authors have attributed male-biased sex ratios in museum collections, and highway mortality victims, to this phenomenon (Shine 1994; Aldridge and Brown 1995; Bonnet et al. 1999). The only previous empirical evidence for the lowered vigilance of reproductive male snakes comes from a field study on Canadian garter snakes, in which the cessation of courtship activity by males coincided with an abrupt increase in their approach distances (Shine et al. 2003). Our study species provides a more robust test of the hypothesis because of the occurrence of same-sized reproductive and non-reproductive males in the same places at the same time of the year. Previous analyses have generally been confounded by seasonal differences, perforce relying on comparisons among reproductive animals in one season and non-reproductive ones in another. The obvious problem with such comparisons is that other seasonally varying factors (such as ambient temperature or vegetation cover) might generate the correlations observed between reproduction and approach distances.

Reproduction affected both locomotor speeds and antipredator responses of female keelbacks. Females that were reproductive (i.e., contained eggs) fled from our approach at a greater distance than did non-gravid animals. These effects cannot be attributed to other differences (e.g., in body size, season, or weather conditions) between reproductive and non-reproductive animals (see above). Instead, our data strongly suggest that reproductive status influenced antipredator responses in female keelbacks.

The abdomens of gravid keelbacks are grossly distended by a clutch that weighs an average of 27% of maternal post-oviposition mass (Brown and Shine 2002). The rigid eggs may also greatly compromise flexibility (and hence locomotor ability) of gravid females. Females burdened with eggs were significantly slower in our raceway trials than were non-reproductive animals. In keeping with this result, viviparous natricine colubrids with a similar degree of physical burdening by the clutch also display reduced maternal mobility (Seigel et al. 1987; Brodie 1989). Gravid lizards with similarly heavy burdens shift their antipredator tactics in response (Bauwens and Thoen 1981; Schwarzkopf 1994; Qualls and Shine 1998) and we suggest the same interpretation for keelbacks (see also Brodie 1989). However, the actual effect on approach distances will depend upon the biology of the specific study system. For example, the viviparous lizards studied by Bauwens and Thoen (1981) remained within their normal home ranges throughout pregnancy, and females reduced their vulnerability to predation by remaining close to shelter. Our keelbacks did not have this option; as egg-layers, the females must move long distances to suitable nesting areas on the dam wall (where we encountered them). Female keelbacks cannot rely upon proximity to shelter, because they must search actively for oviposition sites. Thus, the lowered mobility of gravid females translates into a reduction in approach distance in some systems (reliance upon crypsis in gravid viviparous lizards that can remain close to shelter), but has the opposite effect (an increase in approach distance) for oviparous snakes that must travel across open spaces to search for oviposition sites. That is, female keelbacks burdened with eggs are less capable of evading a predator through speed and, because they will often be far from cover, must flee before the predator approaches close enough to be a major threat. To our knowledge, the only other explanation offered for reproduction-induced shifts in antipredator tactics of female snakes involves active defense of the young in some highly venomous viperid species (Graves 1989; Greene et al. 2002). This explanation is implausible for the non-venomous keelbacks, which are generally very reluctant to bite even when seized.

Our data on these small tropical snakes thus offer a particularly clear example of the impact of reproductive status on an organism's antipredator behavior. In particular, they show that such effects may be manifested very differently in males and females, with the sexes displaying opposite effects and disparate causal links. The shift in antipredator response by females may be a mechanism

to compensate for the locomotor deficit imposed by carrying a litter of eggs in the abdomen. The shift in anti-predator response by males is not a result of any change in locomotor ability, but may instead be due to a change in alertness or responsiveness. One implication of this result is that generalities about “costs of reproduction” are likely to prove elusive: even within a single study population, in a habitat where confounding variables either are minimal or did not influence antipredator tactics, we nonetheless found strong intersexual divergence in the way in which reproductive state influenced an animal’s vulnerability to predation. Shifts in antipredator tactics of keelbacks may serve to reduce the survival cost associated with reproduction for females, but increase the cost for males.

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