



## Risks and rewards: balancing costs and benefits of predator avoidance in a fiddler crab

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The decision to take risks in the presence of a predator involves complex trade-offs between immediate survival and future reproduction. Individuals may gain fitness advantages if they are able to optimally alter their risk-taking strategies depending on the differential costs and benefits of risky behaviours across contexts. Male fiddler crabs (*Austruca mjobergi*) exhibited a higher propensity to take risks in the presence of a female compared with conspecifics that were not presented with a female during both mating and nonmating periods. Contrary to predictions, however, risk-taking behaviour did not differ between mating and nonmating periods.

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An individual's propensity to take risks in the presence of a predator can have significant consequences for its survival and reproduction. Many factors affect risk-taking behaviour, such as size (Shine, Olsson, LeMaster, Moore, & Mason, 2000), age (Seress, Bokony, Heszberger, & Liker, 2011), sex (Franklin, Squires, & Stuart-Fox, 2014; Hazlett & Rittschof, 2000), population density, season (Boukhriss & Selmi, 2010) and the presence of potential mates (Reaney, 2007). Many individuals, when faced with a predator, will seek safety in a refuge (Martín & López, 1999). Once in a refuge, however, an individual begins to pay costs, which it must trade off with the benefit of predator avoidance in order to decide when to re-emerge (Jennions, Backwell, Murai, & Christy, 2003). For example, an individual that remains in a refuge for a prolonged period pays the cost of lost foraging, courting and mating opportunities, while an individual that emerges too soon may pay with its life (Backwell, Jennions, Passmore, & Christy, 1998; Lima & Dill, 1990). Studies across many taxa have shown that such trade-offs are key drivers of risk-taking behaviour (reviewed in Lima & Dill, 1990). Furthermore, when in a refuge, an individual cannot observe the predator and hence, plays a 'waiting game' in which it

must decide when the risk of attack has passed and it is safe to re-emerge (Hugie, 2003).

If there are differential fitness benefits to taking risks across contexts, it may be of adaptive value for an individual to be able to flexibly adjust their risk-taking behaviour (Coleman & Wilson, 1998). For example, during mating periods, it may be beneficial for individuals to conduct risky behaviour in the presence of a predator as there is a higher likelihood of gaining reproductive benefits as well as the benefits of feeding and defending territories (Hazlett & Rittschof, 2000). During nonmating periods, however, it may be more beneficial to reduce risk-taking behaviour as the main activities at this time, feeding and defending territories, may not outweigh the potential predation costs of mortality and lost opportunities for future reproduction (Martín, López, & Cooper, 2003). Differences in the nature and number of benefits gained across mating and nonmating contexts may, therefore, lead to variation in risk-taking behaviour.

Population density can also affect an individual's perception of predation threat and subsequent risk-taking behaviour (the risk assessment hypothesis; Peacor, 2003). For example, at high population densities, it may be more beneficial to conduct risky behaviour in the presence of a predator compared with low population densities, since the competition for resources is higher and the risk of predation is reduced by a high number of conspecifics (Guariento, Carneiro, Esteves, Jorge, & Caliman, 2015; Hamilton, 1971; McCoy, 2007).

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The aim of this study was to examine risk taking in response to a simulated avian predator fly-by (simulating the low-flying swoop over crab habitat performed by avian predators during attack) across contexts in male fiddler crabs, *Austruca mjoebergi*, a species that has previously been shown to exhibit behavioural flexibility in risk-taking behaviour (see Reaney, 2007). We tested risk-taking behaviour across three contexts: (1) mating versus nonmating periods; (2) female presence; (3) population density. Within each context, we tested two components of risk taking in response to a simulated predator fly-by, namely, whether or not an individual chose to take refuge in their burrow and, if so, the latency before the individual re-emerged following the simulated fly-by.

We predicted that, following a simulated predator fly-by, (1) crabs would be more likely to stay above ground, but if they took shelter in their burrow, they would re-emerge sooner during the mating period than during the nonmating period due to the relative potential benefit of reproduction during the mating versus nonmating period, (2) crabs presented with females during the mating period would exhibit the lowest propensity to take refuge in their burrows and, if they took shelter, they would emerge sooner than any other treatment due to the immediate mating opportunity, and (3) crabs in higher local population densities would be more likely to stay above ground during a predator fly-by and, if they were scared into their burrow, they would re-emerge sooner than would conspecifics living at lower densities due to the higher risk of competition and lower risk of predation at high population densities.

## METHODS

We studied a population of *A. mjoebergi* from September to December 2011 at East Point Reserve, Darwin, Northern Territory, Australia (12°24.53'S, 130°49.85'E). *Austruca mjoeburgi* is a small (carapace width <15 mm) crab that lives in dense populations on intertidal mudflats. Both sexes occupy and defend territories containing a burrow, which is used as a mating site (Reaney & Backwell, 2007) and as a refuge from predators (Reaney, 2007). When an avian predator approaches, crabs run back to their burrow entrance and enter the burrow if the threat persists (Backwell, O'Hara, & Christy, 1998); after a short time, the crab will re-emerge and continue to feed or court.

### Trial Protocols

We randomly placed quadrats (a 35 × 35 cm thin metal frame) within the population. We placed small markers at the entrance to each burrow (toothpick with numbered label) within the quadrat. To elicit a predator response, we 'flew' an artificial bird over the quadrat using a manual pulley system running between two stakes that were 3 m apart. The bird model was initially 2.5 m away from the quadrat and at a height of 1 m. It moved to a position that was 15 cm beyond the quadrat and at a height of 20 cm above the ground. Using a triple-event stopwatch, we started the time measurement once the bird model had flown over the quadrat and reached its resting place 15 cm beyond. We noted the time that the first three males within the quadrat re-emerged from their burrows. Re-emergence was determined as the moment that the male had fully emerged from his burrow (100% of the crab could be seen; no part was still in the burrow entrance).

We ran two types of trials during the mating period (5–8 days during the semilunar neap tides): one as described above ( $N = 21$  quadrats), and the other with a female tethered in the centre of the quadrat ( $N = 19$  quadrats). We collected a mate-searching female from a different area of the population and glued a piece of cotton thread onto her carapace using cyanoacrylate (superglue). The

other end of the thread was tied to a nail that was pushed into the sediment, preventing the female from leaving the area but allowing her to move within a 2 cm radius of the nail. We also ran trials during the nonmating period (6–9 days of spring tides every 2 weeks of the semilunar cycle) when the crabs are surface-active but do not engage in mating behaviour ( $N = 20$  quadrats).

No plots were used more than once. After each trial, we captured the three focal males and measured their carapace widths and major claw lengths. The males were returned to their burrows after measurements. Following trials, the tethered female was released to continue mate searching.

No ethics approval was required for this study. Handling was kept to a minimum. No crabs were injured during the research. Work was conducted under a research permit from the Darwin City Council.

### Statistical Analyses

To investigate the effect of treatment, density, male claw length and claw type (fixed effects) on the time it took for males that retreated into their burrows to re-emerge, we produced a mixed-effects Cox proportional hazards survival model. Random intercepts were fitted for each experimental plot to control for nonindependence of data from crabs in the same plot. Statistics were carried out using the 'coxme' package (Therneau, 2019) in R v.3.6.0. We created a logistic mixed-effects regression with a logit link to investigate factors affecting the proportion of crabs not entering their burrows after the simulation. The fixed effects were treatment, claw size, claw type and density of plot; plot identity (ID) was included as a random effect to account for potential pseudoreplication. The impact of fixed effects was assessed using Wald's tests based on parameter estimates and confidence intervals. We ran a mixed-effects Cox survival model of time to re-emergence for those crabs that retreated to their burrows in response to the simulated predator fly-by.

## RESULTS

We recorded re-emergence times following a predator fly-by for 48 males within 21 plots during the mating period, for 47 males within 19 plots during the nonmating period when a female was tethered in the centre of the quadrat and for 53 males within 20 plots during the nonmating period (it was not always possible to capture all the males after each trial). Males that remained above ground following a predator fly-by were recorded as having spent 0 s in their burrows. The mean ( $\pm$ SD) time that males spent inside their burrows was 79.40  $\pm$  78.83 s during the nonmating period, 68.69  $\pm$  57.93 s during the mating period and 20.36  $\pm$  33.40 s during the mating period and with a female tethered in the plot

**Table 1**

Results of a mixed-effects Cox survival model analysing the effect of mating and nonmating periods, female presence, local population density and claw length on the latency of crabs to re-emerge from their burrows following a simulated predator fly-by

Variable	$\beta$	$z$	$P$	$e^\beta$
Treatment [mating period]	0.105	0.24	0.81	1.111
Treatment [tethered female]	2.143	4.24	<b>&lt;0.0001</b>	8.525
Density (male crabs/plot)	0.1885	1.56	0.12	1.207
Claw length (mm)	-0.055	-1.51	0.13	0.947
Claw type [regenerated]	-0.617	-1.40	0.16	0.540

The treatment factor has three levels and, hence, the two coefficients reported here are compared to the base level: treatment [nonmating period]. Random intercepts were fitted for each experimental plot to control for nonindependence of data from crabs in the same plot. Statistics were carried out using the 'coxme' package (Therneau, 2019) in R v.2.15.0. Significant  $P$  values (<0.05) are shown in bold.

(Table 1, Fig. 1). Males living at different population densities did not significantly vary in their responses to the predator fly-by, although crabs at high population densities tended to spend less time in their burrows following a predator fly-by than did conspecifics at low densities (Table 1).

Approximately 17% (25/146) of all tested males did not retreat into their burrow, and instead remained on the surface of the mudflat, despite the predator simulation. This was most notable for the males who were exposed to a tethered female during the mating period, with 36% (17/47) remaining on the surface, compared to 4% of males not exposed to a tethered female during the mating period and 12% of males tested during the nonmating period. The difference between tethered and mating period treatments was significant ( $\beta = -4.426$ ,  $z = -2.108$ ,  $P = 0.035$ ) but not between tethered and nonmating period treatments ( $\beta = -2.463$ ,  $z = -1.384$ ,  $P = 0.166$ ), and no other factors had a significant effect on the probability of remaining on the surface.

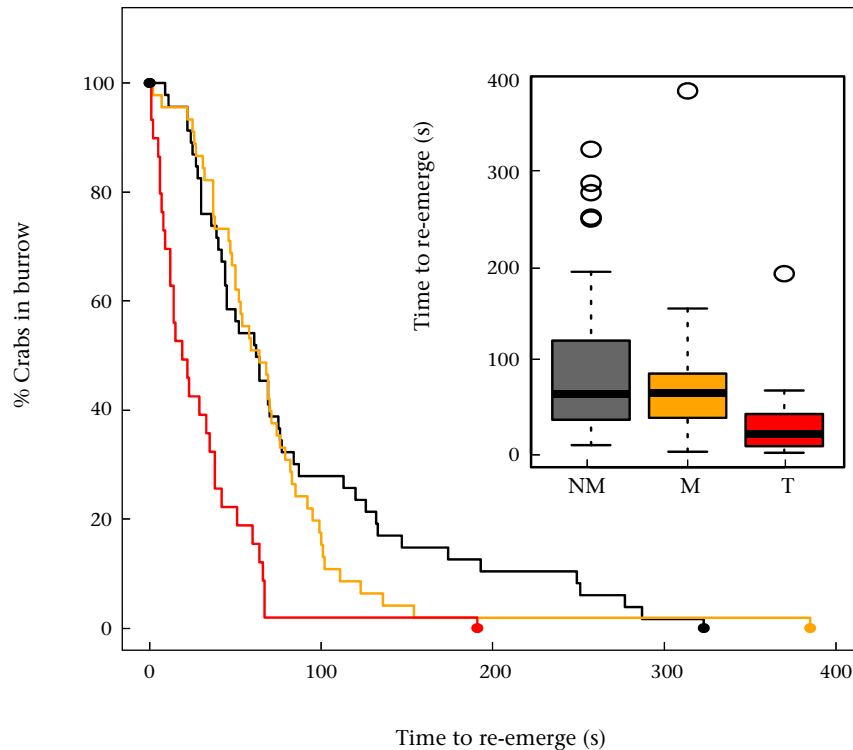
**DISCUSSION**

Male crabs presented with a female during the mating period were more likely to stay above ground during simulated predator fly-bys than were males that were not presented with a female, both during the mating and nonmating periods. Furthermore, males that were scared into their burrows by the simulated predator fly-by during the female presentation treatment emerged significantly faster than did males in any other treatments. There was no significant difference in the likelihood to stay on the surface, nor the latency to re-emerge if scared into their burrow during a predator fly-by among males that were not presented with a female in the mating versus nonmating period. Across all treatments, size had no effect on the likelihood to stay on the surface nor the latency to re-emerge following a simulated predator fly-by. Males living at

high and low local population densities did not differ in their likelihood to stay on the surface, nor their latency to re-emerge if they retreated into their burrow during the simulated fly-by. Below, we consider possible explanations for divergence in risk-taking behaviour across contexts.

During the mating period, fiddler crabs are faced with a trade-off decision between survival and reproduction. The high propensity of male fiddler crabs to take risks under the threat of predation in the presence of a female may be explained by the benefit of an increased likelihood of reproductive opportunities when in the direct presence of a female compared with mating and nonmating scenarios where a female is not in close proximity to a male's burrow. Similar to our findings, male Iberian rock lizards, *Lacerta monticola*, exhibit a higher propensity to take risks under predation threat when presented with a female compared with when no female is present (Martín et al., 2003). Also, males do not alter their courting behaviour (do not exhibit risk-averse behaviour) in response to predators during mating opportunities in hermit crabs, *Clibanarius vittatus* (Hazlett & Rittschof, 2000), and dumpling squid, *Euprymna tasmanica* (Franklin et al., 2014).

Several other factors may drive an individual to prioritize a current mating opportunity over predator avoidance, such as when the chance of future reproduction is low, or when there is a substantial energetic cost to mating (Franklin et al., 2014; Jennions et al., 2003). These factors may be relevant to fiddler crabs as their courtship display, which involves repeated waving of a significantly oversized claw (the major claw can be more than 30–40% of the males body mass) and darting to and from their burrows, is energetically costly (Crane, 1975). It is possible that male crabs were responding to the presence of a female near their burrows as a threat, in the form of a nest usurper, as opposed to a potential mate. This is very unlikely in *A. mjoebergi*, however, since non-mate-searching females of this species do not take over males'



**Figure 1.** The percentage of male crabs that re-emerged from their burrows at a given time (a crab that remained above ground had a re-emergence time of 0) and the time to re-emerge from their burrows following a simulated predator fly-by separated by treatment: NM = nonmating period (grey); M = mating period (orange); T = presence of a tethered female (red).

nests and behave identically to mate-searching females (Peso, Curran, & Backwell, 2016). Furthermore, while we may not be able to incontrovertibly decipher a male's motivation to take more risks in the presence of a tethered female, our results reveal that males are able to flexibly adjust risk-taking behaviour and have a higher propensity to take risks when there is more to lose, in this case, a potential mating opportunity. If the propensity of males to take risks in the presence of a female can be explained by reproductive benefits outweighing the potential risks of predation, why did we not see a difference in risk-taking behaviour between the mating and nonmating periods? Male fiddler crabs may exhibit the same risk-taking strategy across nonmating and mating periods due to the rarity of receptive females in the population and, hence, a consistently low likelihood of mating opportunities.

In fiddler crabs, male–male competition is high as the operational sex ratio is considerably male biased: 11 surface-active males to each female (Reading & Backwell, 2007). Males attract females using a highly conspicuous waving display in which they repeatedly wave their brightly coloured, oversized claw, often in synchrony with nearby males (Clark & Backwell, 2015). The ratio of waving males to mate-searching females is profoundly skewed: 45 males for each female (Reading & Backwell, 2007). Hence, if the likelihood of mating for an *A. mjoebergi* male is always low, even in the mating period, there is no benefit to be gained from males increasing their risk-taking behaviour during this time. A previous study of risk taking in *A. mjoebergi* supports this prediction: during the mating period, receptive females were rare and males were less inclined to take risks unless a female was tethered near to their burrows (Reaney, 2007). The study by Reaney (2007), however, also found that the foraging activity of males was higher in the nonmating period than in the mating period, which contradicts our findings.

The nature of mate searching in *A. mjoebergi* may also contribute to similar risk-taking behaviour of males during the mating and nonmating periods. In many species, males increase their activity during the mating period as they move through the population to seek out mating opportunities. In such cases, males may gain a fitness advantage (through the increased likelihood of mating opportunities) by continuing to be highly active, even when faced with a predator. During the mating period in *A. mjoebergi*, however, females wander through the population searching for males while males remain near their burrow, waiting to court any passing females (Reading & Backwell, 2007). Hence, it may be disadvantageous for a male to increase his risk-taking activities during the mating period unless a female is in direct proximity of a male's burrow when a predator fly-by occurs. This hypothesis is supported by our finding that male *A. mjoebergi* exhibited the highest increase in their risk-taking behaviour when in the direct presence of a tethered female.

We found that crabs living at high local population densities were no more likely to take risks in the presence of a predator than were conspecifics living at lower population densities. This is interesting since activity often increases with larger group sizes in the presence of a predator. Furthermore, in contrast to our findings, variation in risk-taking behaviour occurs among high versus low population densities in *Uca beebei*: males decrease their mate-searching rate at high population densities in the presence of a predator (deRivera, Backwell, Christy, & Vehrencamp, 2003; Smith & Awan, 2009; Van Buskirk, Ferrari, Kueng, Napflin, & Ritter, 2011).

The lack of variation in risk-taking behaviour of *A. mjoebergi* at high and low population densities may be due to the scale at which individual crabs assess the density of conspecifics. For example, we examined the overall population density, whereas an individual crab may respond to more localized cues of conspecific density, such as the presence of close neighbours when making risk-taking

decisions. It is also possible that males use the vibrations of nearby males moving on the surface as nonvisual cues that a predator has passed and it is safe to re-emerge. Indeed, if males can use vibrational cues of surface movement, it may be an interesting contributing factor to explain the increased emergence of males during a simulated predator fly-by in the presence of tethered females. The effect of neighbour presence and density of near neighbours and surface activity on individual risk-taking decisions in the presence of a predator would be an interesting avenue of future study.

Our data revealed that fiddler crab males adjust their risk-taking behaviour in the presence of a simulated predator across different mating and nonmating contexts. Adjustment of risk taking under predation threat appears to be based on the costs and benefits of risky versus safe behaviour within each context, suggesting that male crabs are able to assess complex trade-offs associated with survival and reproduction.

### Data Accessibility

Raw data from this study are available at <https://protectau.mimecast.com/s/5TYUCjZrzqHOxL6QHWsYIM?domain=datadryad.org>.

### Author Contributions

P.R.Y.B. designed the experiments and contributed to the manuscript draft. J.G. drafted the manuscript and assisted with data organization. A.K. conducted statistical analysis.

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### Declaration of Competing Interest

We have no competing interests.

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### References

- Backwell, P., Jennions, M., Passmore, N., & Christy, J. (1998). Synchronized courtship in fiddler crabs. *Nature*, *391*, 31–32. <https://doi.org/10.1038/34076>.
- Backwell, P. R. Y., O'Hara, P. D., & Christy, J. H. (1998). Prey availability and selective foraging in shorebirds. *Animal Behaviour*, *55*, 1659–1667. <https://doi.org/10.1006/anbe.1997.0713>.
- Boukhriss, J., & Selmi, S. (2010). Risk-taking by incubating rufous bush robins *Cercotrichas galactotes*: Season-dependent incubation stage effect. *Journal of Ethology*, *28*, 331–337. <https://doi.org/10.1007/s10164-009-0189-1>.
- Clark, H. L., & Backwell, P. R. Y. (2015). Temporal and spatial variation in female mating preferences in a fiddler crab. *Behavioral Ecology and Sociobiology*, *69*, 1779–1784. <https://doi.org/10.1007/s00265-015-1990-1>.
- Coleman, K., & Wilson, D. S. (1998). Shyness and boldness in pumpkinseed sunfish: Individual differences are context-specific. *Animal Behaviour*, *56*, 927–936. <https://doi.org/10.1006/anbe.1998.0852>.
- Crane, J. (1975). *Fiddler crabs of the world* (Ocyrodidae: genus *Uca*). Princeton, NJ: Princeton University Press.
- deRivera, C. E., Backwell, P. R. Y., Christy, J. H., & Vehrencamp, S. L. (2003). Density affects female and male mate searching in the fiddler crab, *Uca beebei*. *Behavioral Ecology and Sociobiology*, *53*(2), 72–83. <https://doi.org/10.1007/s00265-002-0555-2>.
- Franklin, A. M., Squires, Z. E., & Stuart-Fox, D. (2014). Does predation risk affect mating behavior? An experimental test in dumpling squid (*Euprymna tasmanica*). *PLoS One*, *9*, 14. <https://doi.org/10.1371/journal.pone.0115027>.
- Guariento, R. D., Carneiro, L. S., Esteves, F. A., Jorge, J. S., & Caliman, A. (2015). Conspecific density affects predator-induced prey phenotypic plasticity. *Ecosphere*, *6*, 1–12. <https://doi.org/10.1890/es15-00142.1>.

- Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology*, *31*, 295–311. [https://doi.org/10.1016/0022-5193\(71\)90189-5](https://doi.org/10.1016/0022-5193(71)90189-5).
- Hazlett, B. A., & Rittschof, D. (2000). Predation–reproduction conflict resolution in the hermit crab, *Clibanarius vittatus*. *Ethology*, *106*, 811–818. <https://doi.org/10.1046/j.1439-0310.2000.00604.x>.
- Hugie, D. M. (2003). The waiting game: A 'battle of waits' between predator and prey. *Behavioral Ecology*, *14*, 807–817. <https://doi.org/10.1093/beheco/arg054>.
- Jennions, M. D., Backwell, P. R. Y., Murai, M., & Christy, J. H. (2003). Hiding behaviour in fiddler crabs: How long should prey hide in response to a potential predator? *Animal Behaviour*, *66*, 251–257. <https://doi.org/10.1006/anbe.2003.2190>.
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*, 619–640. <https://doi.org/10.1139/z90-092>.
- Martin, J., & López, P. (1999). When to come out from a refuge: Risk-sensitive and state-dependent decisions in an alpine lizard. *Behavioral Ecology*, *10*, 487–492. <https://doi.org/10.1093/beheco/10.5.487>.
- Martin, J., López, P., & Cooper, W. E. (2003). Loss of mating opportunities influences refuge use in the Iberian rock lizard, *Lacerta monticola*. *Behavioral Ecology and Sociobiology*, *54*, 505–510.
- McCoy, M. W. (2007). Conspecific density determines the magnitude and character of predator-induced phenotype. *Oecologia*, *153*, 871–878. <https://doi.org/10.1007/s00442-007-0795-y>.
- Peacor, S. D. (2003). Phenotypic modifications to conspecific density arising from predation risk assessment. *Oikos*, *100*, 409–415. <https://doi.org/10.1034/j.1600-0706.2003.12043.x>.
- Peso, M., Curran, E., & Backwell, P. R. Y. (2016). Not what it looks like: Mate-searching behaviour, mate preferences and clutch production in wandering and territory-holding female fiddler crabs. *Royal Society Open Science*, *3*, 160339. <https://doi.org/10.1098/rsos.160339>.
- Reading, K., & Backwell, P. (2007). Can beggars be choosers? Male mate choice in a fiddler crab. *Animal Behaviour*, *74*, 867–872. <https://doi.org/10.1016/j.anbehav.2006.09.025>.
- Reaney, L. T. (2007). Foraging and mating opportunities influence refuge use in the fiddler crab, *Uca mjoebergi*. *Animal Behaviour*, *73*, 711–716. <https://doi.org/10.1016/j.anbehav.2006.05.022>.
- Reaney, L. T., & Backwell, P. (2007). Risk-taking behavior predicts aggression and mating success in a fiddler crab. <https://doi.org/10.1093/beheco/arm014>.
- Seress, G., Bokony, V., Heszberger, J., & Liker, A. (2011). Response to predation risk in urban and rural house sparrows. *Ethology*, *117*, 896–907. <https://doi.org/10.1111/j.1439-0310.2011.01944.x>.
- Shine, R., Olsson, M. M., LeMaster, M. P., Moore, I. T., & Mason, R. T. (2000). Effects of sex, body size, temperature, and location on antipredator tactics in free-ranging garter snakes (*Thamnophis sirtalis*, Colubridae). *Behavioral Ecology*, *11*, 239–245.
- Smith, G. R., & Awan, A. R. (2009). The roles of predator identity and group size in the antipredator responses of American toad (*Bufo americanus*) and bullfrog (*Rana catesbeiana*) tadpoles. *Behaviour*, *146*, 225–243. <https://doi.org/10.1163/156853909x410757>.
- Therneau, T. M. (2019). *coxme: Mixed Effects Cox Models (R package version 2.2-14)*. <https://CRAN.R-project.org/package=coxme>.
- Van Buskirk, J., Ferrari, M., Kueng, D., Napflin, K., & Ritter, N. (2011). Prey risk assessment depends on conspecific density. *Oikos*, *120*, 1235–1239. <https://doi.org/10.1111/j.1600-0706.2010.19311.x>.