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# Latitudinal Variation in Lifetime Survival and Reproduction in a Burying Beetle

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Latitudinal Variation in Lifetime Survival and  
Reproduction in a Burying Beetle

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A thesis submitted to the faculty of  
Brigham Young University  
in partial fulfillment of the requirements for the degree of  
Master of Science

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## ABSTRACT

### Latitudinal Variation in Lifetime Survival and Reproduction in a Burying Beetle

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Temperature variation experienced across a latitudinal range is tied to changes in lifespan and life history across multiple taxa. Two patterns of adaptation to latitudinal temperature variation have been documented – counter-gradient (or co-gradient) variation, and local adaptation. To determine how natural selection has shaped life history variation in a burying beetle, *Nicrophorus orbicollis*, we quantified lifetime patterns of reproduction in two populations that represent the geographic and temperature extremes occupied by the species. Lifetime reproduction was quantified at two temperatures that represented conditions typical for each population. Burying beetles from different extremes of their geographic range show considerable variation in lifetime survival and reproduction at different temperatures. Patterns are generally consistent with the local adaptation hypothesis. However, at the higher temperature both populations have lower and equal numbers of offspring over a lifetime. High temperatures may create a constraint on offspring production because of the increased cost of maintaining the food source against bacterial decomposition. This temperature constraint on reproductive success may partially explain the absence of burying beetles from tropical environments, and may predict reductions in latitudinal range as global climate change proceeds.

Keywords: life-history, cost of reproduction, dispersal, adaptation, latitudinal variation

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## INTRODUCTION

All organisms invest energy into growth, somatic maintenance and reproduction. Where energy is limited, investment into any life history component must be at the expense of the other, competing, life history demands (Cole 1954, Gadgil and Bossert 1970, Stearns 1992, Reznick et al. 2000). Allocation among competing demands creates a trade-off between reproduction and other life-history components, and among reproductive efforts over time (i.e., investment in current reproduction decreases energy available for future reproduction; Williams 1966, Reznick 1985, 1992). Natural selection favors individuals that maximize their lifetime reproductive success by appropriately balancing the allocation of time and energy between current and future reproductive efforts (Saether et al. 1993; Heimpel and Rosenheim 1995; Rosenheim 1999; Stearns 1992; Roff 2002). However, the appropriate balance among competing life history demands depends on environmental conditions that influence the acquisition and use of energy and thereby select for specific reproductive patterns over an organism's lifetime.

When differing selective environments drive diversification between populations, different patterns of trait variation can result. There are two adaptive hypotheses that predict patterns of trait variation across selective environmental gradients. The first, counter-gradient variation, occurs when harsh environmental conditions impede the development of a phenotypically plastic trait and selection increases investment to that trait to counteract the negative environmental effects (Conover and Schultz 1995). In a reciprocal transplant design, counter-gradient variation manifests itself as a more rapid development or higher output of the selected trait both in the native and novel environments by the population from the harsh or inhibitory environment. Such

gradients in environment are frequently associated with latitude (Pöykkö and Tammaru 2010, Conover and Present 1990). Co-gradient variation occurs when populations that evolve under favorable conditions exhibit increased trait expression across all environments (Conover et al. 2009). Both counter-gradient and co-gradient variation would thus be observed as parallel reaction norms in which one population outperforms the other across treatments. The second pattern of trait variation across environments is local adaptation (Kawecki and Ebert 2004). Local adaptation arises when each population is adapted to the unique conditions that occur in their local environment. Local adaptation patterns are manifest as crossing reaction norms in a reciprocal transplant design where individuals perform better in their native environment compared to individuals not native to the location. Many studies have investigated patterns of trait expression in traits such as growth (Nylin and Gotthard 1998, Conover et al. 2009); however, few studies have investigated patterns of lifetime reproduction and survival across a latitudinal gradient.

The burying beetle, *Nicrophorus orbicollis*, is an excellent model for studies of variation in lifetime reproductive patterns across a latitudinal gradient. Burying beetles reproduce on small animal carcasses which serve as the sole source of food for both parents and offspring making control and assessment of available resources simple and easily quantifiable. *Nicrophorus orbicollis* are found in the midwest and eastern United States ranging from southern Canada to northern Texas, and they are reproductive throughout the summer (Scott 1998, Wilson et al. 1984, Anderson 1982). Thus, they experience a wide range of temperatures during the reproductive season across their range.

To determine how latitudinal location and associated temperature variation affect patterns of life history variation in *N. orbicollis*, we quantified survival and lifetime patterns of reproduction in two populations from the latitudinal extremes of their range at two temperatures. We tested for patterns consistent with local adaptation, co-gradient variation, or counter-gradient variation in survival, lifetime reproductive output, reproductive allocation through time, and brood failure.

## METHODS

### *Nicrophorus orbicollis* Natural History

*Nicrophorus orbicollis* raise their offspring on small vertebrate carcasses, which serve as the sole food source for both parents and developing larvae. The outcome of competition for carcasses is determined by size of the competitors – larger beetles almost always dominate the carcass (Bartlett and Ashworth 1988; Müller et al. 1990; Creighton 1995). The dominant pair buries the carcass, removes all fur or feathers, shapes the carcass into a ball, and coats it with anal and oral secretions, which inhibit bacterial decomposition (Hall et. al 2011). Before and during the preparation of the carcass, the pair will mate repeatedly. Eggs are subsequently deposited in the soil around the carcass. Larvae move onto the carcass after hatching and are fed via regurgitation of processed carcass material by the parents until larvae are large enough to feed from the carcass themselves. Additionally the parents provide care in the form of carcass defense and maintenance, and defense of the brood from predation. Care of offspring is generally bi-parental, however either parent can successfully raise the brood unaccompanied. The larvae pass through three instars before burrowing into the soil to pupate. Larvae generally arrive on the carcass five days after the carcass is discovered and pupate around five days later with the total time from initial discovery of the carcass to pupation generally lasting about eleven days. All parental care occurs on the carcass and in the burial chamber allowing simulation of conditions found in the field within the laboratory (Smiseth et al. 2003, 2005).

## Experimental Design

To determine if there are differences between populations of *N. orbicollis* and whether they support a local adaptation, co-gradient or counter-gradient pattern we recorded total lifespan for both reproductive and non-reproductive beetles, and lifetime offspring counts from both populations at two distinct temperatures in a common-environment/ pseudo-reciprocal transplant design. The experimental temperatures reflected the mean air temperature during the breeding season for each of the two populations. The full experiment (reflecting the two temperatures) could not be run simultaneously due to restrictions on available lab space, so we ran two sequential experiments – one for each temperature treatment. All other factors excluding temperature remained constant between experiments.

For both common environment experiments, *N. orbicollis* were trapped from the same locations in Oklahoma (35°41'48.3"N 94°48'39.8"W) and Wisconsin (44°37'48.0"N 88°36'00.0"W) during the summer using pitfall traps baited with aged chicken. Mean summer air temperature at the Wisconsin location is 19.3°C, (range 12.9-25.7°C). Mean summer air temperature at the Oklahoma location is 25.8°C (range 19.7-31.8°C; [ncdc.noaa.gov](http://ncdc.noaa.gov) accessed on 1/3/2015). Wild individuals were brought into a controlled environment at Brigham Young University and allowed to breed (on 20-30g mouse carcasses) to generate laboratory-raised individuals for experiments. Upon eclosion, new beetles were placed individually in small plastic containers and fed raw chicken liver *ad libitum* and maintained on a 14L : 10D cycle at 22°C. Date of eclosion was designated as day 0 for all age-based calculations.

At 28 days post-eclosion, females produced in the lab and without previous reproductive experience were randomly assigned to one of three treatments: reproductive 30g (females provided with 30-g ( $\pm 1.0$  g) carcasses), reproductive 20g (females provided with a 20-g ( $\pm 1.0$  g) carcasses), and non-reproductive (females not permitted to reproduce). Both 20-g and 30-g carcasses were used because there can be differing patterns of investment based on carcass size (Creighton et al. 2009). Females were assigned to treatments randomly with respect to body size (width of the pronotum), and there was no significant difference in mean female size between experiments (i.e., temperature treatments,  $P=0.74$ ), between populations ( $P=0.43$ ) or among carcass treatments ( $P=0.70$ ).

At the beginning of each reproductive bout, females were measured and weighed, assigned to an unrelated, sexually mature male, and placed in a small, plastic container containing a mouse carcass and around 6 cm of commercially obtained topsoil. Males were removed 48 hours after introduction to isolate the reproductive effort of the female. Female parenting behavior is not negatively affected by removal of the male in *Nicrophorus orbicollis* (Rauter and Moore 2004, Scott 1990). All crosses were checked daily to monitor the activity of the female, carcass preparation and use, and the progress of the bout. A daily record was kept regarding: number of eggs observed, the number of larvae arriving on the carcass, the developmental stage of the larvae on the carcass, when the larvae disperse to pupate, and death of the female.

To determine if differences between populations or treatments are due to different allocation strategies through time, we recorded the number of offspring and the mean offspring size for each reproductive bout. There was no difference in mean offspring size

between populations ( $P=0.51$ ) or treatments ( $P=0.15$ ) so we did not consider this response variable in the final analysis. When larvae were found to have dispersed from the burial chamber into the surrounding soil to pupate, all larva were counted, weighed, then re-introduced to their container of origin to pupate. The female was removed, measured and weighed, and then placed in a small plastic container with *ad libitum* food for 48 hours. After 48 hours she was placed on a new carcass with a sexually mature male, all measurements were taken as previously described and the cycle repeated until the death of the female. Non-reproductive females were measured and weighed at 28 days, then placed in small plastic containers and fed *ad libitum* food until death at which point life span was recorded.

#### Statistical Analysis

Lifespan and lifetime number of offspring were analyzed in a general linear model (Proc GLM; SAS Institute Incorporated, Cary, NC, USA). Predictor variables were temperature (two levels), population of origin (two levels), and treatment (three or two levels; analysis of lifetime number of offspring did not include the non-reproductive treatment). Female size was included as a covariate for lifetime number of offspring. All interactions (2-way and 3-way) were included in the model.

Initial number of offspring per bout and final number of offspring per bout were analyzed as a repeated measures design (Proc Mixed; SAS Institute Incorporated, Cary, NC, USA). Predictor variables were temperature (two levels), population of origin (two levels), treatment (two levels), and time, indexed as reproductive bout (four levels). All interactions (2-way, 3-way, and 4-way) were included in the model.

Probability of successful reproduction was analyzed as a repeated measures design with a binary response function – either the brood was successful or it failed (Proc Glimmix; SAS Institute Incorporated, Cary, NC, USA). Predictor variables were temperature (two levels), population of origin (two levels), treatment (two levels; 20-g or 30-g carcasses), and time indexed as reproductive bout (four levels). Inclusion of interaction terms was evaluated using AIC scores. The best model included all two-way interactions among temperature, population of origin, and reproductive bout (time), but no 3-way or 4-way interactions. Carcass treatment (carcass sizes of 20-g or 30-g) was included as a main effect, but no interactions with treatment were in the best-fit model. All analyses were run using SAS version 9.33 (SAS Institute Incorporated, Cary, NC, USA).

## RESULTS

### Lifespan and Lifetime Offspring Production

Temperature and treatment (but not location of origin) had a significant effect on lifespan. In addition, all 2-way interactions, but not the 3-way interaction, were significant (Table 1). In general, beetles lived about two weeks longer at the cool temperature treatment, and non-reproductive beetles lived a little over 50% longer than beetles in reproduction treatments. There was no difference in lifespan between beetles on 20-g or 30-g carcasses. At the cool temperature, non-reproductive beetles from both locations had equally long lifespans, and they lived 40-60 days longer than reproductive beetles. At the cool temperature, reproductive beetles from Wisconsin lived about 20 days longer than reproductive beetles from Oklahoma. At the warmer temperature, reproductive beetles from both locations did not differ in lifespan; however, non-reproductive beetles from Oklahoma lived about 38 days longer than reproductive beetles, but non-reproductive beetles from Wisconsin lived only about 18 days longer than reproductive beetles (Figure 1).

### Lifetime Reproductive Success

Temperature and location (but not carcass size) had a significant effect on lifetime offspring number, and the interaction between temperature and location was significant (Table 2). Wisconsin females at the cooler temperature treatment produced about 45 offspring and Oklahoma females producing about 30, but at the warmer temperature treatment beetles from both locations produced about 17 offspring (Figure 2).

### Initial and Final Offspring Count

Temperature treatment and reproductive bout were both significant predictors of initial offspring count per brood. There were significant interactions of carcass size by bout, temperature by carcass by bout, and location by carcass by bout (Table 3). All treatments showed a steady decline in offspring number for the first three bouts with the exception of the warm Oklahoma treatment (Figure 3).

Temperature and reproductive bout were also significant for final offspring count (post culling) per brood. There were interactions of carcass size by reproductive bout and temperature by location by bout (Table 4). As with the initial offspring count there were significant declines in offspring count for each of the first three reproductive bouts in every treatment except the warm Oklahoma treatment, which shows no decline (Figure 4).

### Probability of Brood Success

The likelihood of producing a successful brood for a given bout is significantly influenced by interactions for both location by bout and location by temperature treatment. (Table 5). At the cooler temperature, Wisconsin beetles were significantly more likely to produce a successful brood ( $.99 \pm .06$ ) with each attempt than were Oklahoma beetles ( $.85 \pm .20$ ) whereas the opposite pattern was observed at the warmer temperature treatment with Oklahoma ( $.91 \pm .20$ ) outperforming Wisconsin ( $.68 \pm .24$ ) (Figure 5).

## DISCUSSION AND CONCLUSIONS

The overall patterns that we observe from these two populations of *N. orbicollis* do not reflect patterns of co-gradient variation or of counter-gradient variation, but rather local adaptation with constraint. Local adaptation was manifest in multiple ways. Reproductive *N. orbicollis* from Wisconsin stock lived longer and were more fecund than were their counterparts from Oklahoma at the Wisconsin temperature regime. Reproductive *N. orbicollis* from Oklahoma were no longer-lived or fecund than those from Wisconsin stock at the Oklahoma temperature regime, but they were longer lived when non-reproductive. The advantage shown by Wisconsin beetles at their native temperature regime is obvious given that they lived longer than Oklahoma beetles allowing more total reproductive attempts and thus more total offspring (Williams 1966). However, the advantage had by the Oklahoma beetles may not be as obvious as they at no point enjoyed a clear superiority to Wisconsin beetles in terms of lifetime reproduction because such superiority was only observed in non-reproductive individuals. It was not unexpected that both populations showed reduced non-reproductive lifespan in the warmer treatment because ectothermic organisms at higher temperatures frequently show increased metabolic rate and shorter lifespan (Liu and Walford 1972, Kauler and Hildegard 2011, Kelly et al. 2013), but the difference between populations at the warmer temperature is likely highly adaptive in this system.

Despite having no impact on the reproductive success of the beetles in this study, increased non-reproductive lifespan could have significant fitness consequences in natural systems. Our study was conducted under presumably ideal conditions for reproduction in beetles. Beetles were provided with *ad libidum* food and a constant

supply of mates and suitable carcasses. In wild populations food, mates, and suitable carcasses may not be readily available (Scott 1998). If higher temperatures and associated increase in metabolic rate reduce the time available for finding any or all of the aforementioned resources it would likely have a profound impact on the overall fitness of the organism (Bullock 1955). Thus, while the lifespan difference in non-reproductive females in the lab did not increase reproductive success it is quite likely that this difference is adaptive and an indication of local adaptation in burying beetles.

Both populations displayed phenotypes that are likely to increase overall fitness at temperatures approximating those found in their native habitat while showing no superiority in the opposite environment. The probability of producing a successful brood shows a clear crossing reaction norm indicative of local adaptation. Both populations performed best at their native temperature regime and were outcompeted in their non-native regime. Lifespan, total lifetime fecundity and probability of successfully producing a brood are all characteristics with real and often direct effects on fitness and all appear to be under selection based on temperature in *N. orbicollis*. While both populations are most suited to their native temperature regime there is evidence that selection in some of these traits is be limited by constraint.

The constraint shown here is the lack of ability to increase reproductive lifespan at the warmer treatment. Oklahoma beetles show an increased life expectancy when non-reproductive at warm temperatures when compared to Wisconsin beetles, thus adaptation to the non-reproductive costs of living at higher, Oklahoma temperatures does occur even if the effects are not entirely counteracted. However, when reproducing at the same temperature the disparity between the populations disappears. Both populations are

equally successful and the success rate for both populations is lower than for Wisconsin beetles at their native temperature regime. The elevated cost of reproduction likely comes from the preparation and preservation of a carcass at higher temperatures where bacteria and fungus are able to colonize and grow more rapidly (Jacques 2009). Despite the apparent ability of Oklahoma beetles to reduce temperature related survival costs, there is no evidence that they can reduce reproductive costs at their warmer, native temperature regime.

The cost of reproduction is, in fact, higher for Oklahoma beetles at both temperature treatments. Both populations live for the same amount of time when reproducing at the warmer temperature, thus it may appear that both experience an identical lifespan cost of reproduction. Despite having statistically identical reproductive lifespans, the lifespan cost of reproduction is proportionately higher for Oklahoma beetles at the warmer temperature as well because the non-reproductive lifespans of the two populations are not equivalent. Given that Oklahoma beetles show increased longevity at the warmer temperature when not reproducing, but show no difference in mean lifespan when reproductive means that the actual cost of reproduction in terms of potential lifespan is far greater for Oklahoma beetles at both temperatures. Because the warmer environment is, by all measures, the harsher of the two environments this would be, to some degree, an example of co-gradient variation.

*Nicrophorus orbicollis* are capable of modifying brood size in response to the volume of the carcass provided (Creighton 2005). Previous studies had observed differences life history strategy when female *N. orbicollis* were provided 20g carcasses versus 30g carcasses (Creighton et al. 2009). We, however, did not observe any

significant difference between carcass size treatments for either population at any temperature treatment run. The important factor for predicting longevity was, therefore, only if the beetles were reproducing or not reproducing.

*Nicrophorus orbicollis* from Oklahoma, despite an increased non-reproductive lifespan and being more likely to produce a successful brood, do not appear to be able to reduce the cost of reproduction they incur at warmer temperatures. Costs associated with carcass preparation and preservation could play a role in determining temperature regimes where cross-generational persistence is possible in this species and perhaps across burying beetles. Reproduction appears to become more costly and less profitable at high temperatures (Jacques 2009). For *N. orbicollis* there is no evidence that the cost of reproduction at warmer temperatures can be reduced either behaviorally or physiologically. Thus, it stands to reason that there is likely a threshold temperature at which reproduction may no longer be possible in this species.

The global climate is changing at a rate unmatched by any previous period and looks to continue changing for the foreseeable future (IPCC 2007). Increasing temperatures associated with global climate change are altering environments and species distributions around the globe (Walther et al. 2002, Parmesan and Yohe 2003, Parmesan et al. 1999, Thomas and Lennon 1999, Austin and Rehfisch 2005, Root et al. 2003, Parmesan 2006) and it is unclear if many organisms will be able to adapt rapidly enough to persist particularly within their current geographical ranges (Visser 2008). If adaptation to increased temperatures is impossible or too slow to meet the rate of warming many species are likely to lose or alter current distributions as portions of their range become inhospitable. Such changes will likely force polar expansion or extinction

of latitude-limited species and potential loss of elevation-limited species depending on their respective dispersal capabilities (Hickling et al. 2006, Graham and Grimm 1990, Collingham et al. 1996, Pearson et al. 2002). The genus *Nicrophorus* represent a group that may be under considerable stress due to climate change.

*Nicrophorus* is believed to have originated in temperate Eurasia (Peck and Anderson 1985). There are at least 21 New World species, two Holarctic, 49 or more species in the Old World (Sikes and Venables 2013). Of the New World species only a handful are found in Central or South America with three found in the South American Andes, and those found in tropical areas are restricted, almost completely, to cool regions at high altitude (Sikes and Venables 2013). No species have been collected at lower elevations in Panama (Arnett 1946), Costa Rica (Cornaby 1974), El Salvador (Howden and Peck 1972), Brazil (Young 1978, Penny and Arias 1982), or Borneo (Hanski 1983). However, high elevation species were collected in Panama (Arnett 1946), and El Salvador (Howden and Peck 1972). They are also more common at higher altitude regions of the Southwestern United States (McKinnery 1978). Those species found in central and south America likely moved southward during the Last Glacial Maximum (LGM), which occurred 21,000 years ago and was the coldest period to have occurred in the last 100,000 years (Ruddiman, 2001). Subsequent warming has pushed most species back north and marooned those remaining species in South and Central America on high-altitude islands amid inhabitable tropical climates. As global temperatures increase it is increasingly likely that many of these isolated habitats will become inhabitable to burying beetles due to elevated cost of reproduction likely leading to the loss of the affected species. It is also probable that current distributions in the northern hemisphere will be

forced farther north as suitable southerly habitats become more scarce. This could prove particularly detrimental to threatened species such as the endangered American burying beetle (*Nicrophorus americanus*), which shares much of its range with *N. orbicollis* and also breeds during the warmest summer months (Scott 1998). As these species are already in decline, major habitat loss and relocation are likely to further reduce abundance. Speaking particularly of the American burying beetle, which is currently experiencing a considerable population bottleneck, it is quite possible that the remaining diversity would be less capable of making the rapid adaptive changes that may be available to species with which they would compete. If the constraint we observed is in fact common in burying beetles then they are certainly a group of concern in a warming world.

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## TABLES AND FIGURES

Table 1: Analysis of variance table for female lifespan in response to temperature treatment, location of origin, carcass size treatment, and all interactions. Significant effects are bolded.

Source	DF	P-Value
Temperature	1	<b>&lt;.0001</b>
Location	1	0.1958
Carcass	2	<b>&lt;.0001</b>
Temperature x Location	1	<b>&lt;.0001</b>
Temperature x Carcass	2	<b>0.0007</b>
Location x Carcass	2	<b>0.0066</b>
Temperature x Location x Carcass	2	0.3754

Table 2: Analysis of variance table for lifetime number of offspring in response to temperature treatment, location of origin, carcass size treatment, and all interactions.

Significant effects are bolded.

Source	DF	P-Value
Temperature	1	<b>&lt;.0001</b>
Location	1	<b>0.0327</b>
Carcass	1	0.2375
Temperature x Location	1	<b>0.0173</b>
Temperature x Carcass	1	0.8752
Location x Carcass	1	0.8448
Temperature x Location x Carcass	1	0.2642
Pronotum Diameter	1	<b>0.0317</b>

Table 3: Analysis of variance table for initial number of offspring produced per bout in response to temperature treatment, location of origin, carcass size treatment, and all interactions. Significant effects are bolded.

Effect	DF	P-Value
Temperature	106	<b>&lt;.0001</b>
Location	106	0.7618
Carcass	106	0.2964
Bout	178	<b>&lt;.0001</b>
Temperature x Bout	178	0.1901
Location x Bout	178	0.5263
Carcass x Bout	178	<b>0.0174</b>
Temperature x Location x Bout	191	<b>0.0059</b>
Temperature x Carcass x Bout	191	0.118
Location x Carcass x Bout	191	0.1749
Temperature x Location x Carcass x Bout	191	0.2778

Table 4: Analysis of variance table for final number of offspring produced per bout in response to temperature treatment, location of origin, carcass size treatment, and all interactions. Significant effects are bolded.

Effect	DF	P-Value
Temperature	101	<b>&lt;.0001</b>
Location	101	0.9841
Carcass	101	0.2803
Bout	174	<b>&lt;.0001</b>
Temperature x Bout	174	0.2061
Location x Bout	174	0.8688
Carcass x Bout	174	0.0558
Temperature x Location x Bout	188	0.1603
Temperature x Carcass x Bout	188	<b>0.0452</b>
Location x Carcass x Bout	188	<b>0.0164</b>
Temperature x Location x Carcass x Bout	8	0.2043

Table 5: Analysis of variance table for the probability of producing a successful brood in response to temperature treatment, location of origin, carcass size treatment, and two-way interactions (except for carcass size). Significant effects are bolded.

Effect	Df	P-Value
Temperature	227	<b>0.0065</b>
Location	227	0.2366
Temperature x Location	227	<b>0.0028</b>
Bout	227	<b>0.0061</b>
Temperature x Bout	227	0.5610
Location x Bout	227	<b>0.0153</b>
Carcass	227	0.0553

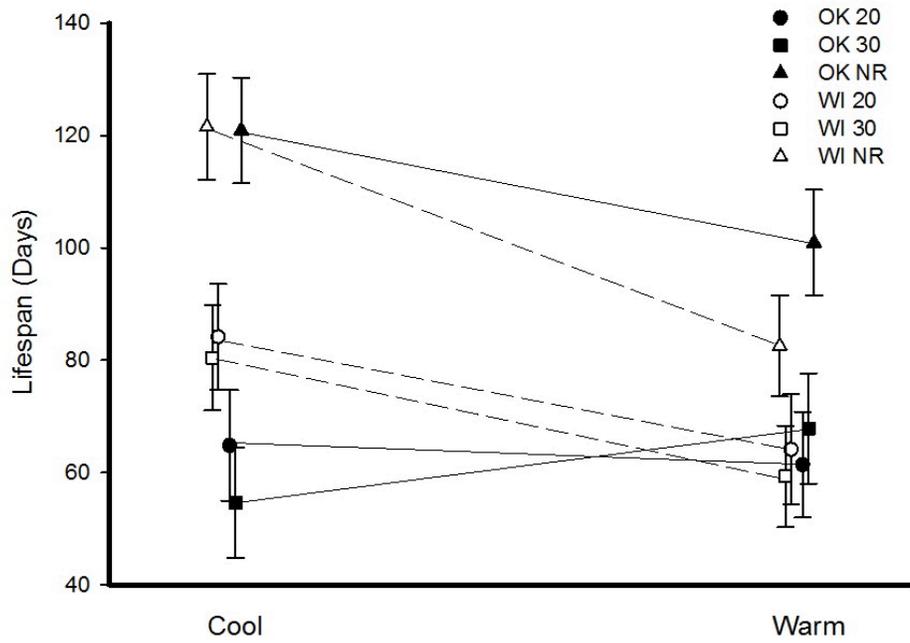


Figure 1: Total lifespan in days of female beetles by population, temperature, and treatment. Oklahoma beetles are depicted in black and Wisconsin beetles as open with the shape depending on the treatment (20g carcasses, 30g carcasses, or non-reproductive). Cool temperature treatments on the left and warm on the right. Error bars represent 95% confidence intervals around the mean.

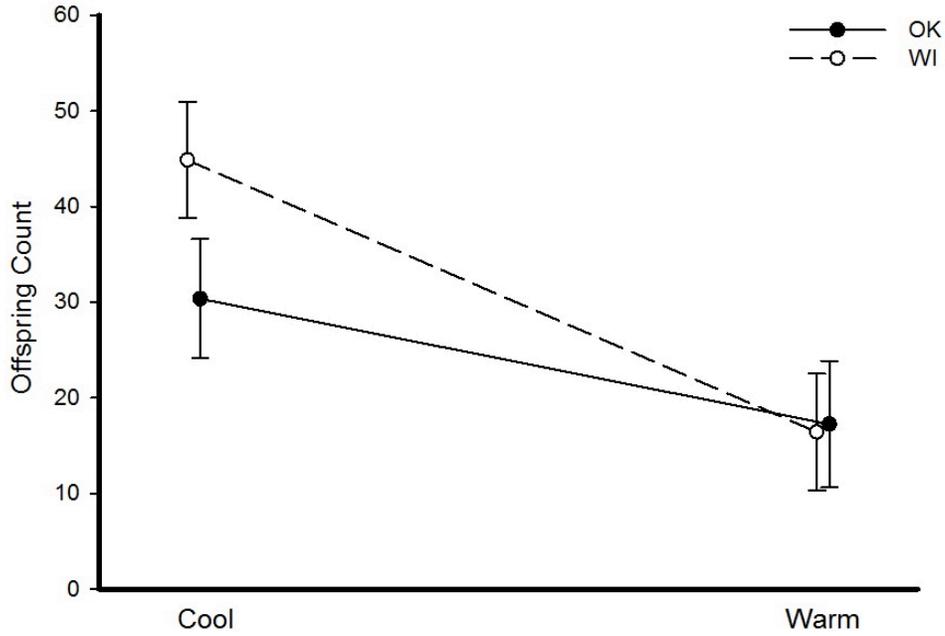


Figure 2: Total lifetime offspring count of female beetles by population and temperature with Oklahoma beetles depicted by black circles and Wisconsin beetles by open circles. Error bars represent 95% confidence intervals around the mean.

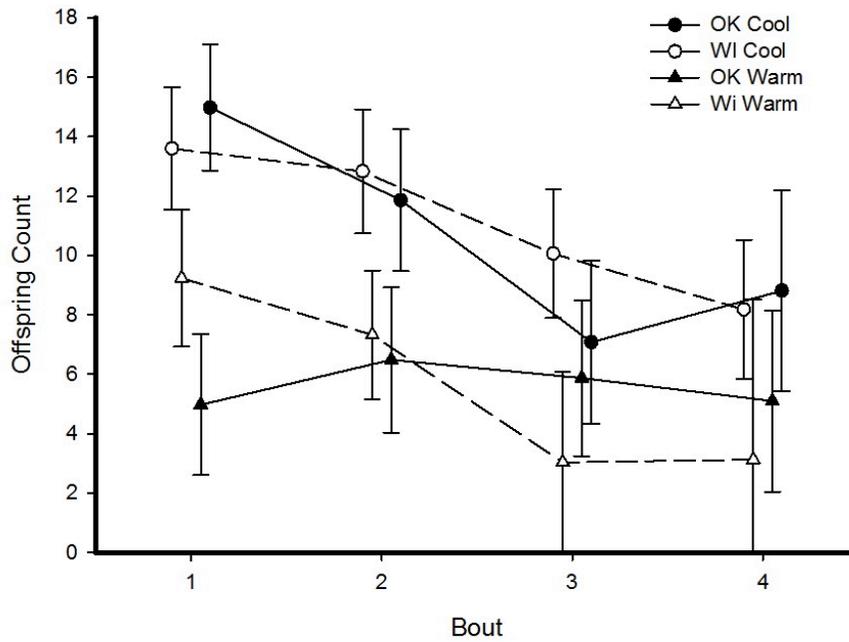


Figure 3: Initial number of offspring per bout by population and temperature; Oklahoma beetles as black and Wisconsin beetles as open shapes with circles indicating cool, and triangles warm temperature treatments. Error bars represent 95% confidence intervals around the mean.

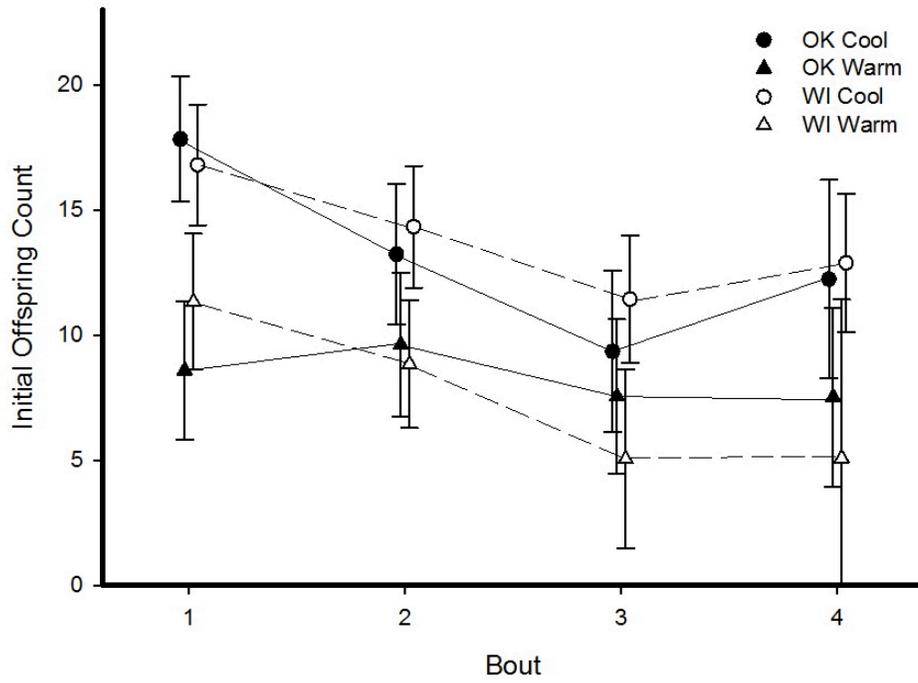


Figure 4: Final number of offspring per bout by population and temperature; Oklahoma beetles as black and Wisconsin beetles as open shapes with circles indicating cool, and triangles warm temperature treatments. Error bars represent 95% confidence intervals around the mean.

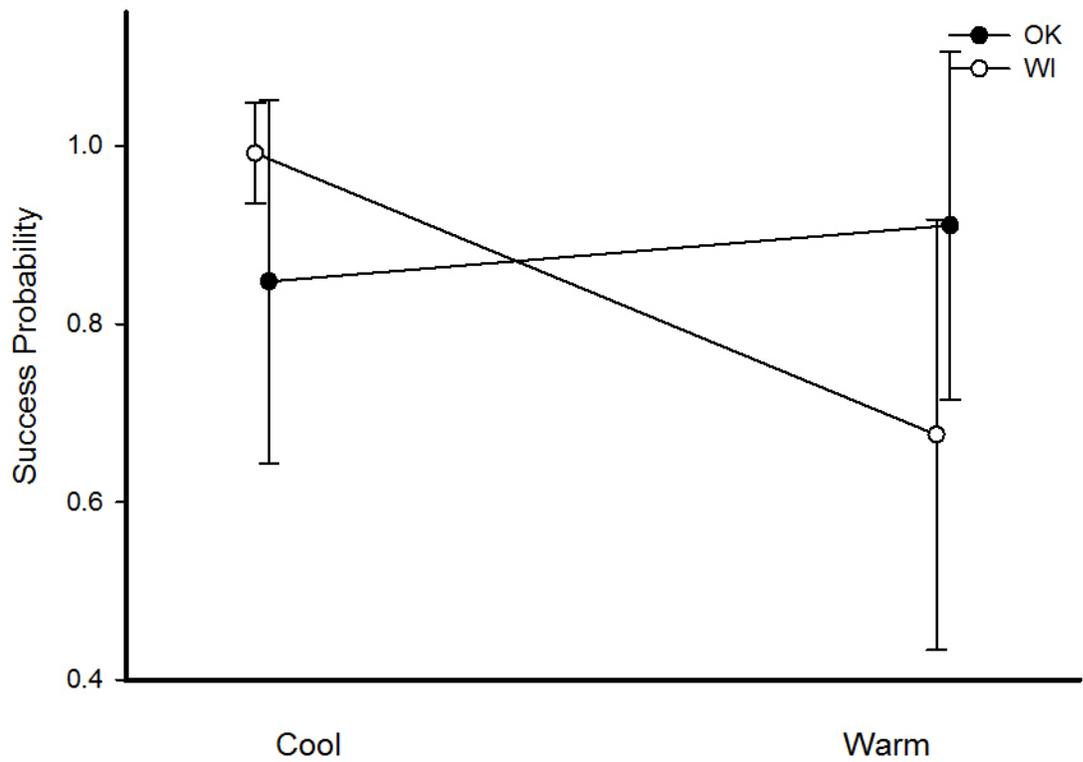


Figure 5: Probability of successful brood with Oklahoma beetles as filled shapes and Wisconsin beetles as open shapes. Error bars represent 95% confidence intervals around the mean.