



UNIVERSITY OF CALGARY

University of Calgary

PRISM: University of Calgary's Digital Repository

Science

Science Research & Publications

2005

Low energy reserves and energy allocation decisions affect reproduction by Mountain Pine Beetles, *Dendroctonus ponderosae*

Elkin, C. M.; Reid, Mary L.

Blackwell Publishing Ltd.

C. M. ELKIN, M. L. REID "Low energy reserves and energy allocation decisions affect reproduction by Mountain Pine Beetles, *Dendroctonus ponderosae*" *Functional Ecology* 2005 19, 102-109

<http://hdl.handle.net/1880/43443>

journal article

Downloaded from PRISM: <https://prism.ucalgary.ca>

Low energy reserves and energy allocation decisions affect reproduction by Mountain Pine Beetles, *Dendroctonus ponderosae*

C. M. ELKIN† and M. L. REID

Department of Biological Sciences, University of Calgary, 2500, University Dr N.W. Calgary, Alberta, Canada T2N 1N4

Summary

1. Low internal energy reserves at the beginning of the breeding season may impose physiological constraints on an animal's reproductive investment and may alter the optimal trade-off between investment in reproduction and somatic condition.

2. Here we examine how the energetic condition of female Mountain Pine Beetles (*Dendroctonus ponderosae*) affects their reproductive investment. We starved beetles to simulate the decrease in energy that accompanies dispersal and tested whether starved beetles had decreased egg number and decreased egg size, or both. We further distinguished whether changes are due to physiological constraints or shifts in allocation between reproduction and somatic condition.

3. We found that starved beetles produced smaller eggs than non-starved beetles, but females were able to partially offset the energetic deficit by feeding at their breeding habitat. Starvation did not decrease the number of eggs beetles produced.

4. The number and size of eggs produced depended on whether females allocated energy to reproduction or to somatic condition. However, this life-history allocation decision was independent of the amount of energy beetles had at the beginning of reproduction.

5. Our results demonstrate the importance of assessing reproductive investment in the context of other life-history trade-offs. Specifically, since egg size in Mountain Pine Beetles was highly dependent on both the amount of energy remaining after dispersal and whether energy was allocated to reproduction or somatic maintenance, we expect both of these trade-offs to be under strong selection.

Key-words: Egg size, life-history trade-off, parental somatic condition, Scolytinae

Functional Ecology (2005) **19**, 102–109

Introduction

The allocation of resources to reproduction or parental somatic condition is a fundamental life-history trade-off (Williams 1966). How females allocate energy should depend on their future reproductive potential and the benefit of increased investment in their current reproductive bout (Trivers 1972; Roff 1992; Stearns 1992). Both of these factors may be influenced by the energetic state of the female (Boggs 1992; Williams & Cooch 1996). Low energy reserves at the beginning of reproduction may impose physiological constraints on an individual's reproductive investment (Jönsson 1997; Glazier 1999; Fox & Czesak 2000) while also altering the costs and benefits of allocation to somatic condition or reproduction (Sibly & Calow 1989; Stelzer 2001). Allocating energy to somatic condition may increase

reproductive efficiency (Boggs 1992) or optimize allocation between current and future reproductive success (Trivers 1972; Maynard Smith 1977). Therefore, an individual's condition may affect reproductive investment both directly through physiological constraints and indirectly through changes in optimal energy allocation. Here we test whether the energetic condition of female Mountain Pine Beetles (*Dendroctonus ponderosae* Hopkins, Coleoptera: Scolytidae) affects the size and number of eggs produced, and distinguish whether any changes in reproductive investment are due to physiological constraints or differences in resource allocation.

The energetic condition of a female may affect both the total amount of energy invested in reproduction as well as the amount of energy invested in individual offspring (Pollock 1997; Bommarco 1998; Stelzer 2001; Koivula *et al.* 2003). Theory predicts that in a given environment there is an egg size that optimizes the trade-off between the number and size of eggs produced

(Smith & Fretwell 1974; Geritz, van der Meijden & Metz 1999; Fox & Czesak 2000). However, if low energy physiologically constrains reproductive investment the optimal egg size may not be achieved (Parker & Begon 1986; Jönsson 1997; Fox & Czesak 2000). Alternatively, egg size may be maintained at the expense of egg number or somatic condition.

The effect of low energy reserves on reproduction will depend on the energy sources animals use to provision offspring (Boggs 1992). Reductions in energy reserves will be particularly important to capital breeders (Drent & Daan 1980; Jönsson 1997). Conversely, in income breeders reproductive investment may be relatively unconstrained by initial energetic condition.

Mountain Pine Beetles are a well-studied species (Rudinsky 1962; Wood 1982) that have an obligatory dispersal flight from their natal habitat to locate breeding habitat, during which time no feeding is known to occur (Atkins 1969; Thompson & Bennett 1971; Anderbrant 1988; Anderbrant & Schlyter 1989). Consequently, there is natural variation in the condition of individuals arriving at breeding habitat. Furthermore, they lay their clutches progressively within the breeding substrate (tree phloem) in well-defined galleries, and the energy used for reproduction could be derived from existing capital energy stores gained in the natal habitat (capital breeding) or energy acquired in the breeding habitat (income breeding). After producing a brood, some female Mountain Pine Beetles leave their first host tree and attempt to achieve a second reproductive bout in another tree (Reid 1958; Wood 1982).

We modified capital breeding energy stores by starving beetles prior to allowing them to reproduce, simulating the decrease in energy that occurs during dispersal (Kinn *et al.* 1994). In another bark beetle, Gries *et al.* (1990) found that starvation and flight cause the same decrease in fat reserves that in turn had the same effect on pheromone production. Placing beetles in logs that differed in phloem thickness and phloem nutrient quality provided variance in energy available for income breeding. By measuring the size and number of eggs produced, and the energetic condition of female beetles before and after reproducing, we test whether low energy reserves constrain reproductive investment, whether Mountain Pine Beetles exhibit a trade-off between investment in reproductive and somatic condition, and whether energetic condition affects how resources are allocated to reproduction or somatic condition.

Materials and methods

PARENT BEETLES

Mountain Pine Beetle parents used in the experiment were collected from field-colonized Lodgepole Pine trees (*Pinus contorta* var. *latifolia* Engelm). We selected two trees from a stand infested with Mountain Pine Beetles near Golden, British Columbia (51.2° N, 116.9° W).

We felled the trees in mid-September 2000, cut the trees into 80-cm logs, and randomly placed the logs in 1-m³ emergence cages in the lab. Emergence cages were kept in a temperature- and humidity-controlled room (temperature ~22 °C, relative humidity ~65%) that was on a 10:14 light : dark cycle. We checked the emergence cages daily to remove all newly emerged beetles, and sexed and measured the size of emerged adults. We measured the pronotum width and total length of beetles to the nearest 0.04 mm using a dissecting microscope with an ocular micrometer. The volume of beetles was calculated using the equation for volume of an ellipsoid.

Males were placed individually in 1.5-ml microcentrifuge tubes that had holes to allow air exchange and a moistened piece of paper towel. They were kept in the dark at 4 °C until they were used. Emerged females were paired according to size, and randomly assigned to either starvation or non-starvation treatments. Non-starved females were housed in the same 1.5-microcentrifuge tubes as males, and held in the dark at 4 °C for 5 days. Females in the starvation treatment were housed individually in 30-ml vials that were lined with moistened paper towel and had holes for air exchange, and were kept at room temperature (~22 °C) on a 10L:14D cycle for 5 days. Larger vials were used for starved beetles to allow for beetle activity.

REPRODUCTIVE INVESTMENT

Parental beetles were implanted into logs taken from two Lodgepole Pine trees felled on 5 January 2001. We cut nine 1-m long logs from each tree, and sealed the logs' cut ends with wax to reduce desiccation. The diameter of the logs ranged from 18.5 to 24.9 cm. The logs were randomly distributed throughout the temperature- and humidity-controlled room that housed the emergence cages.

Following completion of the starvation/non-starvation treatments, we measured the fresh mass of all female beetles to the nearest 0.01 mg. We then implanted female beetles individually near the bottom of the 1 m implantation logs. Females were implanted 10 cm from the bottom of the log, and were spaced 10 cm apart. Implantations were done by placing the female beetle in 1.5-ml implantation chambers that we had sealed to the implantation logs, allowing her to naturally begin excavating an egg gallery. We checked the females after 24 and 48 h; if the beetle had begun excavating into the log we recorded that a gallery had been initiated and added a randomly chosen male. Only males that had emerged within the previous 5 days were used. If excavation had not yet begun by 48 h we recorded the female as not entered, and terminated the replicate. We recorded whether or not beetles successfully entered the logs to see if starved beetles were physiologically restricted even prior to beginning oviposition.

Beetles were allowed to construct egg galleries (see Reid 1958) for 24 days. To measure eggs, we removed

sections of bark that contained part of a beetle's egg gallery. We removed sections twice during the experiment: 10 days after implantation had begun and at the end of the experiment. The timing of data collection balanced the necessity of minimizing the disturbance of the adult beetles but also of collecting eggs prior to them eclosing. Immediately after bark sections were removed from logs they were sealed in plastic bags and frozen. A phloem sample was taken from the base of each gallery and its thickness was measured to the nearest 0.02 mm using a dissecting microscope and ocular micrometer.

Reproductive investment data were collected by recording the position of offspring (larvae and eggs) along the egg gallery and by measuring the size of eggs. The size of the oval Mountain Pine Beetle eggs, measured to the nearest 0.02 mm using a dissecting scope with ocular micrometer, was determined using the length along the longest axis and the width measured perpendicular to the long axis at the mid-point. Egg volume was calculated using the equation for the volume of an ellipsoid.

We determined the energetic condition of female beetles following reproduction by collecting females at the conclusion of the experiment and measuring their fat content. Fat content was measured using petroleum ether extraction (Atkins 1969). Individual beetles were dried at 63 °C for 24 h and their dry mass recorded. Fat was then extracted by immersing dried beetles in 35–60 °C petroleum ether in a Soxhlet apparatus for 8 h. Following fat extraction the beetles were again dried at 63 °C for 24 h, and their dry mass taken. Mass of fat was calculated as the difference in mass before and after fat extraction. We calculated the prereproduction condition of the female beetles, after starvation treatment but prior to reproduction, and the postreproduction condition of female beetles after beetle removal from the implantation logs. We calculated beetle condition using a body condition residual index (Jacob, Marshall & Uetz 1996) that controls for body size. The prereproduction body condition residual index was calculated by regressing the wet body mass of female beetles against their volume and obtaining the residuals; wet body mass was used because we were restricted to using a non-destructive sampling method. The postreproduction body condition residual index was calculated by regressing the mass of fat in female beetles against their volume; mass of fat was used as it is a more direct measure of condition than wet body mass (Rolff & Joop 2002).

To assess if, and how, female beetles modify their somatic condition during gallery construction, we examined the change in condition of starved and non-starved beetles over the course of gallery construction. We calculated the change in each female beetle's condition by subtracting her residual index condition prereproduction from her residual index condition postimplantation. A positive number indicates an increase in the beetle's relative condition.

ANALYSES

Data were tested for normality using a Shapiro–Wilk *W*-test; non-normal data were transformed as necessary. Residuals were examined after fitting models to confirm parametric assumptions. Statistical analysis was performed using JMP 4.1 software (SAS Institute 1996). All means are reported \pm SE.

We tested whether starvation decreased female beetles' energy reserves by analysing females' prereproduction wet weight using a model that included starvation treatment as the primary independent variable and female volume as a covariate. Following reproduction we analysed the mass of fat held by starved and non-starved beetles using the same model. We analysed starved and non-starved females prereproduction condition (body condition residual index) and postreproduction condition using *t*-tests.

Except where noted, we analysed egg size and egg number using general linear models. The principal factors included in the models were starvation treatment, postreproduction condition of the females, and the interaction term between these two factors. These factors allowed us to test how starvation affected reproductive investment, and whether reproduction was related to somatic condition. The interaction term between female postexperiment condition and starvation treatment was explicitly included in all statistical models so we could test whether differences in reproductive investment between beetles resulted from starved beetles investing more of their capital resources into reproduction at the cost of their somatic condition. Therefore, a significant positive interaction term indicates that starved beetles may compensate for poor condition by investing proportionately more of their available energy reserves in reproduction.

Also included in the models were variables specific to the condition of the implantation logs, pertinent to assessing income breeding. Galleries were blocked by which log they were in. Phloem thickness (specific to each gallery) is a measure of food availability (Amman 1972; Amman & Pasek 1986) and was included as a continuous variable to account for differences in resource availability between females. Additional beetle variables included were female volume, and whether or not a male, female or both parent beetles remained within the egg gallery at the termination of the experiment. Our analysis of egg volume included distance along the gallery that the egg was oviposited. We also included the interaction between starvation treatment and distance.

We conducted parallel analyses using female prereproduction condition, instead of starvation treatment, as the factor representing the treatment-induced decrease in energy reserves. For both egg size and egg number using female pre-experiment condition instead of starvation decreased that amount of variance the statistical model explained. Therefore we report the results from models using starvation treatment.

Results

FEMALE CONDITION: PREREPRODUCTION AND POSTREPRODUCTION CONDITION

Starved beetles weighed less prior to reproduction than non-starved beetles ($F_{1,57} = 9.45$, $P < 0.005$; least squared means of wet mass: non-starved 10.8 ± 0.16 mg, starved 10.0 ± 0.19 mg). Prereproduction condition was calculated as the residuals from the regression of wet body mass of female beetles against their volume ($N = 60$, $R^2 = 0.84$, $P < 0.0001$). Starvation treatment decreased beetles' energy reserves: on average, the condition of starved females was less than the condition of non-starved females ($t = 3.09$, $df = 58$, $P < 0.005$; means of residual wet mass: non-starved 0.33 ± 0.16 mg, starved -0.46 ± 0.19 mg), although there was overlap between treatments.

Following reproduction there was no difference in mass of fat reserves held by starved or non-starved beetles ($F_{1,56} = 0.32$, $P = 0.57$; least squared means of mass of fat: non-starved 0.97 ± 0.08 mg, starved 1.05 ± 0.10 mg). We calculated postreproduction condition by regressing the mass of fat in female beetles against their volume ($N = 59$, $R^2 = 0.27$, $P < 0.0001$; one female beetle was destroyed during final gallery excavation and could not be measured). There was no difference between the postreproduction condition of starved and non-starved beetles ($t = -0.57$, $df = 57$, $P = 0.57$; means of residual fat: non-starved -0.03 ± 0.08 mg, starved 0.05 ± 0.10 mg). To confirm that the lack of difference in postreproduction condition of starved and non-starved beetles was not due to changing our metric of condition, we re-ran our analysis using the same index used for prereproduction condition (regression of wet mass *vs* volume). Again we found the postreproduction condition of starved beetles did not differ from non-starved beetles. Thus, starvation treatments did alter the condition of female beetles, but beetles were able to recover some of their somatic condition over the course of gallery construction. Throughout the remainder of the analysis, postreproduction condition was included as the residuals from our regression of mass of fat *vs* volume.

ENTRY SUCCESS

We analysed the entry success of female beetles using a logistic regression model that included starvation treatment and prereproduction female condition (residual index). Starvation treatment did not affect whether or not the female beetles entered the logs ($\chi^2 = 1.15$, $df = 1$, $P = 0.28$), but female beetles that were in poor condition were less likely to enter the logs ($df = 1$, $\chi^2 = 4.27$, $P < 0.05$: condition of females that did not enter, -0.72 ± 0.32 mg; entered females, 0.12 ± 0.13 mg). Starvation treatment remained insignificant when condition was omitted from the model.

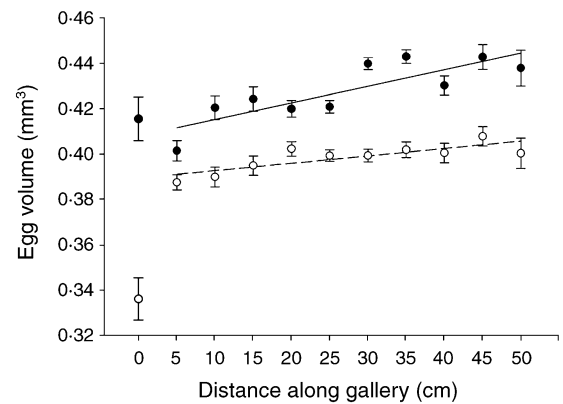


Fig. 1. Size of eggs (least square means \pm SE) produced by \circ starved and \bullet non-starved females, at increasing distance along egg galleries. Regression lines for starved (dashed line) and non-starved (solid line) females are shown. For the purpose of presentation, we divided distance along egg gallery into 5-cm segments and included distance as a nominal variable in the statistical model. Least square means were extracted from this model. Regression lines were fit excluding the data points from the first 5 cm of each gallery (see text for details).

REPRODUCTION

Because we collected eggs during only two sampling periods, eggs from the beginning of a gallery segment were older than eggs at the end of the segment and differences in egg size could possibly be due to egg age. We tested whether egg volume was dependent on egg age by analysing egg volume using a model that included egg age at the time of removal and the absolute distance along gallery, blocking by female. Only galleries for which we had eggs from both the first and second gallery segments were included. Egg age was highly non-significant ($F_{1,473} = 0.003$, $P = 0.95$), indicating that differences in egg volume along the gallery were not due to egg age.

Visual inspection of the data suggested that egg size in the first 5 cm of egg gallery was substantially smaller than egg size in the remainder of the gallery (Fig. 1). Because of this non-linear change in egg size along galleries we performed separate analysis on eggs that were in the first 5 cm and eggs that were past 5 cm. We analysed egg size in the first 5 cm of gallery using a general linear model that included starvation treatment, postreproduction condition of the females, female size and phloem thickness. These variables accounted for 65.4% of the variance in egg volume (whole model: $F_{4,13} = 4.25$, $P < 0.05$). Starved beetles produced smaller eggs than non-starved beetles (Fig. 1, $F_{1,13} = 11.61$, $P < 0.01$). Egg size in the first 5 cm was not affected by females' postreproduction condition ($F_{1,13} = 3.93$, $P = 0.08$), female size ($F_{1,13} = 1.03$, $P = 0.34$) or phloem thickness ($F_{1,13} = 3.25$, $P = 0.11$). We then analysed egg size using a two-way ANOVA that included starvation treatment, location of the eggs in the gallery (first 5 cm of gallery or beyond 5 cm), and the interaction between these variables. We found a significant statistical

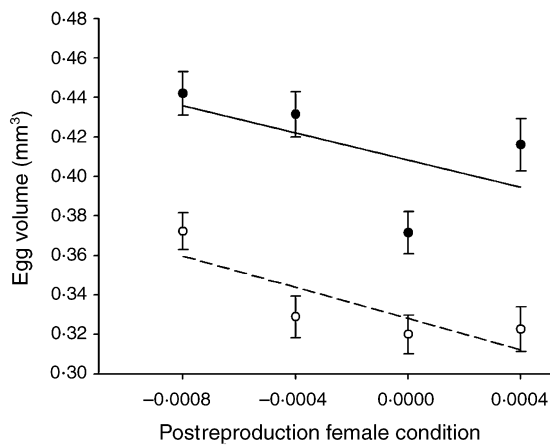


Fig. 2. Size of eggs (least square means \pm SE) produced by \circ starved and \bullet non-starved females that varied in their postreproduction condition. Regression lines for starved (dashed line) and non-starved (solid line) females are shown. For the purpose of presentation, we divided the continuous postreproduction female condition variable and included condition as a nominal variable in the statistical model. Least square means were extracted from this model.

interaction between starvation treatment and whether eggs were before or beyond 5 cm ($F_{3,967} = 5.94$, $P < 0.02$). While still producing smaller eggs, starved beetles increased the size of their egg more between 5 cm and beyond 5 cm than non-starved beetles (Fig. 1).

For the size of all eggs beyond 5 cm, the variables that we measured accounted for 50.2% of the variance in egg volume (whole model: $F_{23,865} = 37.91$, $P < 0.0001$). Starved beetles produced smaller eggs than non-starved beetles (Fig. 2, $F_{1,865} = 28.26$, $P < 0.0001$). Female beetles that were in worse condition at the end of the experiment produced larger volume eggs (Fig. 2, $F_{1,865} = 7.26$, $P < 0.01$), but there was no interaction between starvation treatment and the condition of female beetles at the end of the experiment (Fig. 2, $F_{1,865} = 2.37$, $P = 0.10$). We found a significant statistical interaction between starvation treatment and the distance eggs were located along the gallery (Fig. 1, $F_{1,865} = 13.20$, $P < 0.001$). The rate of increase in egg volume with distance along gallery was greater in non-starved beetles compared with starved beetles (Fig. 1).

Mean egg volume differed between logs ($F_{15,865} = 33.81$, $P < 0.0001$), and beetles reproducing in an area with thicker phloem produced larger eggs ($F_{1,865} = 9.75$, $P < 0.01$). Larger female beetles produced smaller eggs on average than smaller females ($F_{1,865} = 10.17$, $P < 0.001$). Galleries with both male and female beetles present at the end of the experiment produced smaller volume eggs than galleries that just contained females ($F_{1,865} = 71.93$, $P < 0.0001$).

Measured variables accounted for 68.2% of the variation in egg number (whole model: $F_{23,35} = 3.18$, $P < 0.001$). Egg number was not affected by starvation treatment ($F_{1,35} = 0.10$, $P = 0.75$). Beetles that were in worse condition at the end of the experiment produced a greater number of eggs (Fig. 3, $F_{1,35} = 13.80$, $P < 0.001$).

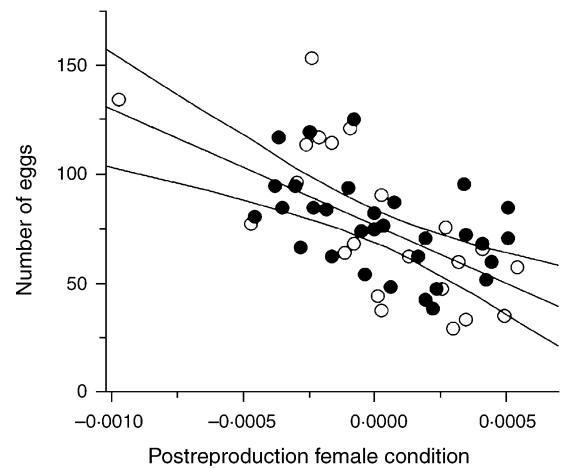


Fig. 3. Leverage plot of number of eggs produced by female beetles that varied in their postreproduction condition (see text): \circ starved beetles, \bullet non-starved beetles. The diagonal lines represent the linear regression fit and associated 95% confidence curves.

There was no interaction between starvation treatment and the condition of beetles following the experiment ($F_{1,35} = 0.16$, $P = 0.67$).

Egg number differed between logs ($F_{16,35} = 2.65$, $P < 0.01$), but phloem thickness did not affect the number of eggs ($F_{1,35} = 0.19$, $P = 0.66$). There was a non-significant trend for larger beetles to produce more eggs ($F_{1,35} = 3.38$, $P = 0.08$). More eggs were oviposited when both males and females remained in the gallery until the end of the experiment ($F_{2,35} = 4.85$, $P < 0.02$).

CHANGE IN FEMALE CONDITION

We analysed the change in beetle condition using a general linear model that included starvation treatment, phloem thickness, log, whether or not a male was present, beetle's cumulative reproductive investment, and an interaction between starvation treatment and cumulative reproductive investment. We calculated females' cumulative reproductive investment, until the experiment was terminated, by multiplying each female's mean egg size by the number of offspring she produced.

The variables accounted for 52.46% of the observed variance in the change in female beetle condition (whole model: $F_{20,32} = 1.95$, $P < 0.05$). Starved beetles improved their condition compared with non-starved beetles (Fig. 4, $F_{1,32} = 5.62$, $P < 0.05$). Female beetles that had smaller cumulative reproductive investment showed an increase in condition compared with beetles that made a larger reproductive investment (Fig. 4, $F_{1,32} = 5.37$, $P < 0.05$). Female beetles therefore improved somatic condition at the expense of reproductive investment. There was no interaction between starvation treatment and the beetle's cumulative reproductive investment ($F_{1,32} = 0.43$, $P = 0.52$). The lack of an interaction between starvation and cumulative reproductive investment indicates that whether beetles

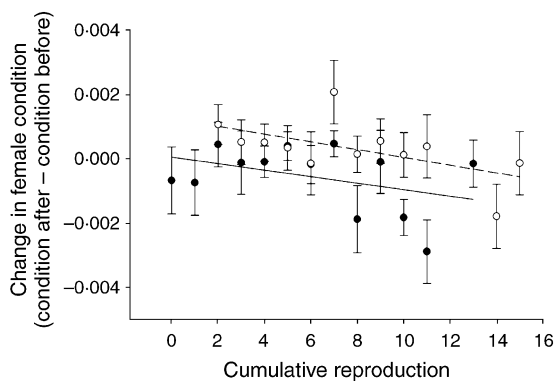


Fig. 4. Change in female condition (least square means \pm SE) in \circ starved and \bullet non-starved beetles that varied in their cumulative reproductive output. Regression lines for starved (dashed line) and non-starved (solid line) females are shown. Cumulative reproductive output was calculated by multiplying female's mean egg size by the number of offspring produced. Change in female condition was calculated by subtracting a beetle's prereproduction condition from its postreproduction condition. For the purpose of presentation, beetles' cumulative reproductive success was transformed and we included cumulative reproduction as a nominal variable in the statistical model. Least-square means were extracted from this model.

allocated resources to somatic condition or reproduction was independent of their initial energetic state. The change in beetle condition was not affected by phloem thickness ($F_{1,32} = 0.10$, $P = 0.755$), did not differ between logs ($F_{15,32} = 1.29$, $P = 0.26$), and was not affected by whether or not a male was present ($F_{1,32} = 1.77$, $P = 0.19$).

Discussion

PHYSIOLOGICAL RESTRICTIONS ON REPRODUCTION

Arriving at a breeding site with low energy reserves decreased the ability of Mountain Pine Beetles to successfully enter host trees, and constrained their reproductive investment, indicating that, to some degree, Mountain Pine Beetles are capital breeders. Starvation decreased egg size but did not decrease the number of eggs produced over the duration of the experiment. Hansen & Bentz (2003) also found that the number of eggs produced by the Spruce Beetle (*Dendroctonus rufipennis* Kirby) was independent of females' lipid content.

Reproduction was also influenced by parental feeding at the breeding site, indicating that Mountain Pine Beetles are also income breeders. Breeding site selection is doubly important for beetles because it determines the environment that larvae will develop in and it also determines the acquisition rate and magnitude of resources that parental beetles can invest in reproduction (Stearn 1992; Jönsson 1997).

Although both starved and non-starved beetles increased egg size along their galleries, the rate of increase was higher in non-starved beetles after the

initial few eggs. The cost of arriving at a tree with low fat reserves is therefore propagated throughout the reproductive bout and restricts the ability of starved beetles to increase egg size by using resources acquired at the breeding sites. Increased size of eggs laid later in a gallery may compensate for deteriorating breeding habitat quality over time (Reid 1962; Amman 1972; Landa 1992; Kawecki 1995), although it may also be related to increased female somatic condition.

Our finding that beetles reproductive investment depended on breeding habitat quality and a female's energetic condition upon arrival at the breeding site indicates that Mountain Pine Beetles experience a trade-off between investment in dispersal and investment in reproduction. Investing more energy in dispersal may improve the quality of breeding habitat that beetles locate (Morris 1992; Stamps 2001), but will limit the amount of energy that beetles can invest in reproduction. The value of investment in dispersal or reproduction will therefore depend on the relative effects that breeding habitat quality and energetic condition have on an individual's fitness (Boggs 1992).

REPRODUCTION AND SOMATIC CONDITION TRADE-OFFS

Beetles improved their somatic condition while egg production was proceeding, implying that there is a benefit to maintaining a base level of somatic condition. Oviposition by Mountain Pine Beetles is an active process, with female beetles excavating egg galleries through the phloem (Reid 1958). If gallery construction rate, or the efficiency of converting phloem to eggs, increases with beetle condition, we would expect Mountain Pine Beetles to allocate resources to improve their somatic condition (Boggs 1992). Alternatively, improved somatic condition may increase the chance of successfully dispersing to a new tree for a second reproductive bout (Reid 1962; Trivers 1972).

Our results indicate that Mountain Pine Beetles make a trade-off between somatic condition and reproductive investment, and that this trade-off encompassed both egg size and number. Whether energy was allocated to reproduction or somatic condition had a large influence on the reproductive components we measured and therefore is likely under strong selection (Stearns 1992). However, allocation to somatic condition and reproduction was independent of the beetles' energetic condition upon arriving at the breeding site. Theory predicts that energy available for reproduction (Boggs 1992; de Jong & van Noordwijk 1992) can alter the current or future reproductive potential of an individual and may therefore influence optimal energy allocation (Jönsson, Tuomi & Järemo 1995; Stelzer 2001). Our results imply that the energetic state of a beetle arriving at a breeding site does not influence its expectation of future reproduction. In Mountain Pine Beetles, and income breeders more generally, the ability to feed at the breeding site may function to disconnect

future reproductive potential from individual's energetic state upon arrival at the breeding site. It remains unclear what factors are driving some beetles to invest more in reproduction at the expense of somatic condition, and presumably of future reproductive success. Future work may attempt to dissect whether some aspect of beetles' internal condition, quality of the host tree for reproduction, or environmental factors encountered by beetles prior to gallery initiation results in Mountain Pine Beetles modifying their current *vs* future reproductive investment.

Acknowledgements

We thank Emile Begin and the British Columbia Forest Service for providing access to trees infested with Mountain Pine Beetles and anonymous reviewers for improving the manuscript. Funding for this research was provided by the Natural Science and Engineering Research Council of Canada (M.L.R.) and the Alberta Conservation Association, Challenge Grants in Biodiversity Program (C.M.E.).

References

- Amman, G.D. (1972) Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *Journal of Economic Entomology* **65**, 138–140.
- Amman, G.D. & Pasek, J.E. (1986) Mountain Pine Beetle in Ponderosa Pine: Effects of Phloem Thickness and Egg Gallery Density. USDA Forest Service Issue no. INT-367. US Department of Agriculture.
- Anderbrant, O. (1988) Survival of parent and brood adult bark beetles, *Ips typographus*, in relation to size, lipid content and re-emergence or emergence day. *Physiological Entomology* **13**, 121–129.
- Anderbrant, O. & Schlyter, F. (1989) Cause and effects of individual quality in bark beetles. *Holarctic Ecology* **12**, 488–493.
- Atkins, M.E. (1969) Lipid loss with flight in the Douglas-fir beetle. *Canadian Entomologist* **101**, 164–165.
- Boggs, C.L. (1992) Resource allocation: exploring connections between foraging and life history. *Functional Ecology* **6**, 508–518.
- Bommarco, R. (1998) Stage sensitivity to food limitation for a generalist arthropod predator, *Pterostichus cupreus* (Coleoptera: Carabidae). *Environmental Entomology* **27**, 863–869.
- Drent, R.H. & Daan, S. (1980) The prudent parent: energetic adjustment in avian breeding. *Ardea* **68**, 225–252.
- Fox, C.W. & Czesak, M.E. (2000) Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology* **45**, 341–369.
- Geritz, S.A.H., van der Meijden, E. & Metz, J.A.J. (1999) Evolutionary dynamics of seed size and seedling competitive ability. *Theoretical Population Biology* **55**, 324–343.
- Glazier, D.S. (1999) Trade-offs between reproductive and somatic (storage) investments in animals: a comparative test of the van Noordwijk and de Jong model. *Evolutionary Ecology* **13**, 539–555.
- Gries, G., Bowers, W.W., Gries, R., Noble, M. & Borden, J.H. (1990) Pheromone production by the pine engraver *Ips pini* following flight and starvation. *Journal of Insect Physiology* **36**, 819–824.
- Hansen, E.M. & Bentz, B.J. (2003) Comparison of reproductive capacity among univoltine, semivoltine, and re-emerged parent spruce beetles (Coleoptera: Scolytidae). *Canadian Entomologist* **135**, 697–712.
- Jacob, E.M., Marshall, S.D. & Uetz, G.W. (1996) Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61–67.
- de Jong, G. & van Noordwijk, A.J. (1992) Acquisition and allocation of resources: genetic (co) variances, selection and life histories. *American Naturalist* **139**, 749–770.
- Jönsson, K.I. (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**, 57–66.
- Jönsson, K.I., Tuomi, J. & Järemo, J. (1995) Reproductive effort tactics: balancing pre- and postbreeding costs of reproduction. *Oikos* **74**, 35–44.
- Kawecki, T.J. (1995) Adaptive plasticity of egg size in response to competition in the cowpea weevil, *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Oecologia* **102**, 81–85.
- Kinn, D.N., Perry, T.J., Guinn, F.H., Strom, B.L. & Woodring, J. (1994) Energy reserves of individual southern pine beetles (Coleoptera: Scolytidae) as determined by a modified phosphovanillin spectrophotometric method. *Journal of Entomological Science* **29**, 152–163.
- Koivula, M., Koskela, E., Mappes, T. & Oksanen, T.A. (2003) Cost of reproduction in the wild: manipulation of reproductive effort in the bank vole. *Ecology* **84**, 398–405.
- Landa, K. (1992) Adaptive seasonal variation in grasshopper offspring size. *Evolution* **46**, 1553–1558.
- Maynard Smith, J. (1977) Parental investment: a prospective analysis. *Animal Behaviour* **25**, 1–9.
- Morris, D.W. (1992) Scales and costs of habitat selection in heterogeneous landscapes. *Evolutionary Ecology* **6**, 412–432.
- Parker, G.A. & Begon, M. (1986) Optimal egg size and clutch size: effects of environmental and maternal phenotype. *American Naturalist* **128**, 573–592.
- Pollock, D.E. (1997) Egg production and life-history strategies in some clawed and spiny lobster populations. *Bulletin of Marine Science* **61**, 97–109.
- Reid, R.W. (1958) The behaviour of mountain pine beetle, *Dendroctonus monticolae* Hopk., during mating, egg laying, and gallery construction. *Canadian Entomologist* **90**, 505–509.
- Reid, R.W. (1962) Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia. II. Behavior in the host fecundity, and internal changes in the female. *Canadian Entomologist* **94**, 605–613.
- Roff, D.A. (1992) *The Evolution of Life Histories: Theory and Analysis*. Chapman & Hall, New York.
- Rolff, J. & Joop, G. (2002) Estimating condition: pitfalls of using weight as a fitness correlate. *Evolutionary Ecology Research* **4**, 931–935.
- Rudinsky, J.A. (1962) Ecology of Scolytidae. *Annual Review of Entomology* **7**, 327–348.
- SAS Institute (1996) *JMP Start Statistics: a Guide to Statistical and Data Analysis Using JMP and JMP IN Software*. Duxbury Press, Belmont, CA.
- Sibly, R.M. & Calow, P. (1989) A life-cycle theory of responses to stress. *Biological Journal of the Linnean Society* **37**, 101–116.
- Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *American Naturalist* **108**, 499–506.
- Stamps, J.A. (2001) Habitat selection by dispersers: integrating proximate and ultimate approaches. *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp. 230–242. Oxford University Press, Oxford.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stelzer, C.P. (2001) Resource limitation and reproductive effort in a planktonic rotifer. *Ecology* **82**, 2521–2533.

- Thompson, S.N. & Bennett, R.B. (1971) Oxidation of fat during flight of male Douglas-fir beetles, *Dendroctonus pseudotsugae*. *Journal of Insect Physiology* **17**, 1555–1563.
- Trivers, R.L. (1972) Parental investment and sexual selection. *Sexual Selection and the Descent of Man* (ed. B. Campbell), pp. 136–179. Aldine, Chicago, IL.
- Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* **100**, 687–690.
- Williams, T.D. & Cooch, E.G. (1996) Egg size, temperature and laying sequence: why do Snow Geese lay big eggs when it's cold? *Functional Ecology* **10**, 112–118.
- Wood, D.L. (1982) The bark and ambrosia beetles of north and central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs No. 6*. Brigham Young University Press, Provo, Utah.

Received 14 May 2004; revised 21 July 2004; accepted 5 August 2004