

# Nutrition, hormones and life history in burying beetles

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## Abstract

Nutrition, hormones and the allocation of physiological resources are intricately related. To investigate these inter-relationships in female burying beetles (*Nicrophorus* spp.), we examined the effect of diet quality on juvenile hormone (JH) levels and reproduction, and the effect of JH supplementation on reproduction and resistance to starvation. *Nicrophorus orbicollis* adult females fed a less preferred mealworm larvae diet gained less body mass, had smaller ovaries and had lower titers of JH in their hemolymph than females fed a preferred blowfly diet. When presented a carcass for breeding, females on a less preferred diet oviposited 33% fewer eggs, and eggs were of 18% less mass. Females on the less preferred diet also took longer to begin oviposition as indicated indirectly by the time when their eggs hatched. To investigate the effects of JH, independent of nutrition, JH was topically applied to single and paired females of *Nicrophorus tomentosus*. When presented a carcass, JH-treated paired females oviposited more eggs (28%—year 1, 44%—year 2) than control females, and also showed a trend toward faster oviposition. JH supplementation had a greater effect on single females. JH treatment increased the proportion of single females attempting reproduction (at least one viable larva), increased the number of eggs (69%—year 1, 123%—year 2), and increased the proportion of females ovipositing early. In separate experiments, treatment with JH or a JH analog negatively affected resistance to starvation in three species. Treatment with JH reduced starvation survival by 10.3% days in *N. tomentosus* females. Treatment with the JH analog methoprene reduced starvation survival 17.8% in *N. orbicollis* females and by 18% in *Ptomascopus morio* females. These results suggest that JH has positive and negative effects on different components of life history.

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**Keywords:** Burying beetle; *Nicrophorus*; Juvenile hormone; Reproduction; Life history; Nutrition

## 1. Introduction

### 1.1. Background

Evolutionary biologists anticipate a negative association between reproduction and survival (Calow, 1979; Roitberg, 1989). This relationship is rarely simple because nutrition, the hormonal state, and the allocation of physiological resources are often tightly correlated. Empirical studies have demonstrated at least three ways in which, contrary to expectation, reproduction and survival are positively rather than negatively correlated. Individuals in a superior nutritional state have more resources for many physiological

needs, therefore obscuring tradeoffs among competing needs (van Noordwijk and de Jong, 1986). Reproduction and survival might also decline in concert in organisms undergoing senescence (Banduriansky and Brassil, 2002). Genetically, a positive reproduction–survival correlation can occur when an individual possesses a risky acquisitive developmental strategy favored in resource rich environments (Reznick et al., 2000). Manipulation studies can be helpful to examine inter-related components of fitness (Ketterson and Nolan, 1992; Tatar and Carey, 1995; Zera and Harshman, 2001), and may provide insight into the genetic basis of an association (Chippindale et al., 1993). Because hormones are often a key mediator of how resources are allocated (Finch and Rose, 1995), hormonal manipulation offers a useful way to separate correlated effects. When both nutritional and hormonal manipulations can be integrated in the same study, we

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have a better chance of achieving an adequate understanding of how an organism devotes limited resources among competing physiological needs.

In adult insects, juvenile hormone (JH) is a primary gonadotropic hormone (Koeppel et al., 1985). Biosynthesis of JH and JH titers are often positively related to nutrition as revealed by experiments employing limited diets or starvation (Tobe and Chapman, 1979; Rouland et al., 1980; Schal et al., 1993; Rankin et al., 1997a,b; Osorio et al., 1998; Yin et al., 1999). Poor nutrition can result in less yolk synthesis in the fat body and/or less uptake of yolk by the ovary (Engelmann, 1970; Glinka et al., 1995). Application of JH can induce reproductive behavior and ovarian development (Schal et al., 1997; Soller et al., 1999; Hancock and Foster, 2000). JH has also been shown to decrease longevity (Herman and Tatar, 2001; Tatar and Yin, 2001). Although manipulation of hormones in studies of both reproduction and survival show promise for understanding how components of fitness interact (Wikelski and Ricklefs, 2001), such studies have rarely been done with JH and insects.

### 1.2. Natural history

When a burying beetle (*Nicrophorus*) female emerges as an adult, it is in a pre-reproductive state with low levels of JH and small ovaries. As an adult female feeds on carrion and larvae of carrion insects, her body mass increases, JH biosynthesis increases, JH titers in the hemolymph rise, and ovarian mass increases (Trumbo, 1997; Scott et al., 2001). Adults that cannot locate carrion or larvae of carrion insects will attempt to prey on other insects (Pukowski, 1933). Starved females have smaller ovaries and maintain low levels of JH (Trumbo et al., 1995). The effect of diet quality on JH and reproduction has not been investigated. After well-fed females obtain reproductive competence, JH titer and ovarian mass level off, and females begin to search for a small, fresh vertebrate carcass (Trumbo et al., 1995). When a female discovers such a carcass, she immediately begins to prepare the resource for her young (bury the carcass, remove hair, round into a ball). JH titer rises quickly and ovaries increase two- to threefold in mass prior to oviposition, which can begin in as little as 16 h (Scott and Traniello, 1987; Trumbo et al., 1995; Scott et al., 2001). These qualitative changes occur whether or not a male is present; quantitative effects of male help on female physiology are poorly understood in these biparental insects. Burying beetles exhibit some of the highest levels of JH found in insects (Trumbo et al., 1995). The rapid physiological responses to discovery of a carcass are hypothesized to be adapted for the ecological need to exploit a valuable resource that can deteriorate quickly if not prepared (Trumbo et al., 1995). Treatment of females with JH

has a slight positive effect on ovarian mass but is not sufficient to induce the two- to threefold increase associated with reproduction, nor is it sufficient to induce oviposition in the absence of a carcass (Scott et al., 2001).

Using burying beetles, we investigated (1) how reproductive performance is related to nutrition, (2) the correlation between nutrition and JH, and (3) the effect of JH supplementation on reproductive performance and survival.

## 2. Methods

### 2.1. Nutrition and reproduction

#### 2.1.1. Preferred diet

To examine the preferred food of burying beetles, 10 *Nicrophorus orbicollis* Say and 10 *Nicrophorus tomentosus* Weber were placed individually in a small round container (9 cm d × 4 cm h) and provided one mealworm larva (*Tenebrio molitor*) and one blowfly larva (*Calliphora* spp.). Each container was checked daily until both food items were eaten.

#### 2.1.2. Weight gain and ovarian growth

To gauge the effect of diet on adults during the pre-reproductive period, *N. orbicollis* females from a laboratory population were isolated at adult emergence, weighed, and then fed one of two diets. Eight females were maintained on the preferred diet (blowfly larvae) and eight on the less preferred diet (mealworm larvae). Each female had access to a mate for a 24 h period on Days 10 and 17. Body mass was measured again on Days 5 and 20. On Day 20, a hemolymph sample was taken and the ovaries were dissected out and weighed. JH titers were quantified as in Trumbo et al. (1995).

#### 2.1.3. Reproductive response

It has been hypothesized that the reproductive physiology of burying beetles is adapted to respond quickly to a rare ephemeral resource (Trumbo et al., 1995). To determine how nutrition affects this response, 34 *N. orbicollis* females were isolated and maintained initially on small scraps of chicken liver. On Day 15, females were set up on either a preferred diet ( $N = 17$ , blowfly larvae) or a less preferred diet ( $N = 17$ , mealworm larvae) for 10 days. All females had access to a mate for a 24 h period on Days 10 and 20. On Day 25, females were presented a 15–18 g carcass in a soil-filled container (18 × 32 × 11 cm) at the onset of scotophase (the beginning of the active period for *N. orbicollis*). After 24 h, three eggs of each female were removed and weighed (one female in the mealworm treatment did not produce eggs and was excluded from the remainder of the experiment). After 84 h, the carcass and female

were removed. Subsequently, the container was examined every 4 h for larvae that had eclosed since the previous check. The time of eclosion provided an indirect measure of the earlier time of oviposition without interfering with female behavior or reproduction.

## 2.2. JH and reproductive performance

We manipulated JH levels in reproductively aged females to determine its effects on reproductive performance. *N. tomentosus* were caught in mid-August in the Naugatuck State Forest in Cheshire, Connecticut during 1999, 2000, 2001 and 2002. Traps were suspended from trees and baited with well-ripened carcasses. Concurrent trapping using fresh, small carcasses placed on the ground indicated that *N. tomentosus* is not breeding at this time (unpublished results). In the laboratory, individuals were housed in mixed sex groups (6–12 individuals) and maintained initially on scraps of chicken liver in containers without soil (to inhibit reproduction). Females were then isolated, their pronotal width and body mass determined, and fed blowfly larvae for 3 days. Experimental females were treated with a topical application of JH III (Sigma-Aldrich Inc.) (400 µg in 2 µl of hexane) 3 days prior and again 12 h prior to presentation of a carcass (hormone treatment). Control females were handled similarly but were given only hexane. A mouse carcass (18–21 g) was presented in a soil-filled container (18 × 32 × 11 cm). The female was placed directly on the carcass, held there for 20 s, and then released under the carcass.

In 1999 and 2000, females were tested while breeding in male–female pairs. Males were isolated for 3 days and fed blowfly larvae but were not treated with hormone or hexane. In 2001 and 2002, females were tested while breeding alone. After 3 days on the carcass, the adult(s) were removed. The container was then checked every 4 h for newly eclosed larvae, indicating the number of viable eggs produced.

## 2.3. JH and starvation resistance

To examine the effect of JH on survival, we applied JH III or the JH analog methoprene (Sandoz Corp.) to females. Females were starved during hormonal manipulation to provide the strongest contrast between JH- and control-treated individuals. Female *N. tomentosus* were trapped in mid-August in 2000 and initially housed in mixed sex groups (15 L: 9 D) and fed chicken liver for 14 days. Females were then isolated in small containers (9 cm d × 4 cm h), provided with moist toweling but no food, and treated with JH III (200 µg in 2 µl hexane;  $N = 12$ ) or hexane alone ( $N = 12$ ) on Days 1 and 6. The mean pronotal width (5.0 mm) and body mass (0.29 g) of treatment and con-

trol beetles were the same. To decrease variation caused by differences in body size, all individuals were within a narrow pronotal size range (4.7–5.2 mm). Checks were made daily to determine survival.

In a separate experiment, female *N. orbicollis* from a laboratory colony were isolated at 21 days of age, fed scraps of chicken liver for 10 days, and then starved as above. Individuals were treated with methoprene (300 µg in 3 µl hexane;  $N = 15$ ) or the equivalent volume of hexane ( $N = 15$ ) on Days 1 and 6. Mean pronotal width (6.6 mm) and body mass (0.43 g) were the same for treatment and control beetles at the time of isolation. To decrease variation caused by differences in body size, all individuals were within a narrow pronotal size range (6.3–6.7 mm). Survival was determined as above.

A third experiment to test the effect of hormone treatment on survival employed a laboratory population of *Ptomascopus morio* Kraatz, a closely related non-parental silphid beetle native to Japan. Adult females were kept in mixed sex groups for 25 days, and then isolated for 7 days and supplied continuously with chicken liver scraps. Females were then weighed and treated with methoprene (100 µg in 1 µl hexane;  $N = 20$ ) or with hexane alone ( $N = 20$ ). Individuals were supplied with a moist paper towel and checked daily.

Survival times were not normally distributed and variances were not equal. A nonparametric Wilcoxon's test was used to analyze survival times in *N. orbicollis* and *N. tomentosus* (SAS, 2000). For the data from *P. morio*, an analysis of covariance was performed using the ranks of body mass and treatment as independent variables and ranks of survival times as the dependent variable.

All statistical analyses were carried out using SAS (2000).

## 3. Results

### 3.1. Nutrition and reproduction

#### 3.1.1. Preferred diet

When beetles were provided with both a mealworm and blowfly larva, every beetle first consumed the blowfly larva (Likelihood Ratio test,  $P < 0.001$ ). Although some beetles took up to 6 days to consume the mealworm larva, all prey were eventually consumed.

#### 3.1.2. Weight gain and ovarian growth

Female *N. orbicollis* maintained on a preferred blowfly diet gained more mass, had larger ovaries, and had higher titers of JH compared to females maintained on the less preferred mealworm diet (Table 1). While the

Table 1  
Effects of nutrition on weight gain and reproductive status of *N. orbicollis* females (means  $\pm$  SE)

Treatment	Initial mass (g)	Weight gain (g)		Ovary mass (mg)	JH titer (ng/ml)
		Day 5	Day 20	Day 20	Day 20
Mealworm diet ( $N = 8$ )	0.32 (0.05)	0.045 (0.014)	0.060 (0.015)	6.4 (1.1)	128 (24)
Blowfly diet ( $N = 8$ )	0.31 (0.04)	0.078 (0.009)	0.120 (0.012)	12.3 (1.0)	265 (41)
ANOVA ( $df = 14$ )		$F = 4.23, P = 0.06$	$F = 9.60, P = 0.008$	$F = 14.0, P = 0.002$	$F = 7.20, P = 0.02$

mealworm diet was adequate to maintain body weight, weight gain was minimal (15% over 20 days) and ovaries were small.

### 3.1.3. Reproductive response

A female insect in a poor nutritional state might respond to a reproductive opportunity in one of three ways. She might oviposit fewer eggs, oviposit smaller eggs, or take longer to begin oviposition. We found that *N. orbicollis* females responded in all three ways. Females on the less preferred mealworm diet oviposited 33% fewer eggs (Fig. 1a) and eggs were 18% lighter in mass (Fig. 1b) as compared to females on the preferred blowfly diet. Females on the less preferred diet were also less likely to produce eclosing larvae within 100 h of discovery of a carcass (Fig. 2;  $P < 0.001$ , Likelihood Ratio  $\chi^2 = 13.05, P < 0.001$ ).

## 3.2. JH and reproductive performance

### 3.2.1. Single females

Treatment with JH significantly affected whether a single female produced at least one viable egg (Fig. 3) and also increased the number of viable eggs (Fig. 4). There was significant inter-year variation for both measures. JH treatment also increased the number of females producing a larva within 72 h (indicating how quickly oviposition was initiated) (Fig. 5; Wald  $\chi^2$  test:  $\chi^2_{\text{YEAR}} = 0.44, P_{\text{YEAR}} > 0.20, \chi^2_{\text{TREATMENT}} = 4.97, P_{\text{TREATMENT}} = 0.029$ ).

### 3.2.2. Pairs

JH treatment did not have a significant effect on whether or not a paired female *N. tomentosus* produced at least one viable egg (Fig. 3); paired females in both treatments almost always produced at least a few eggs. JH-treated females breeding in pairs produced more viable eggs than control-treated females (Fig. 4). The inter-year variation was also significant. The number of females producing larvae by 72 h was marginally affected by treatment and significantly affected by year (Fig. 6; Wald  $\chi^2$  test:  $\chi^2_{\text{YEAR}} = 5.87, P_{\text{YEAR}} = 0.015, \chi^2_{\text{TREATMENT}} = 3.44, P_{\text{TREATMENT}} = 0.064$ ). JH treatment did not, however, cause the fastest responding females to oviposit sooner. For both single females and pairs, the first larvae hatched between 64 and 68 h after carcass discovery, regardless of hormone treatment.

## 3.3. JH and starvation resistance

JH significantly reduced the survival time in days (10.3%) of *N. tomentosus* females as compared to controls (Fig. 7,  $P < 0.05$ , Wilcoxon's test). Similarly, treatment with the JH analog methoprene reduced the survival time (17.8%) of *N. orbicollis* females as com-

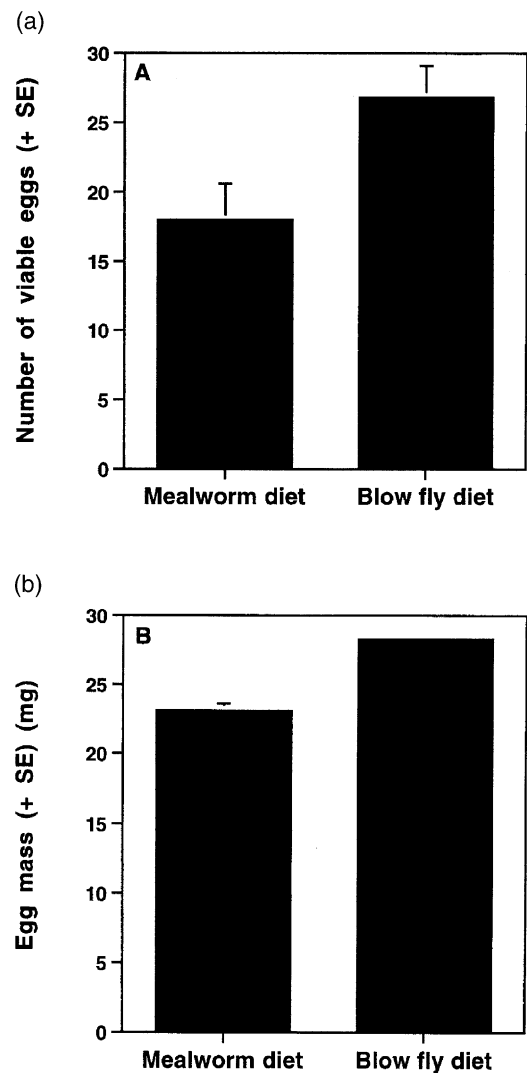


Fig. 1. The mean ( $\pm$ SE) number of viable eggs (a) and egg mass (b) from *N. orbicollis* females maintained as adults on a diet of mealworm larvae ( $N = 16$ ) or blowfly larvae ( $N = 17$ ). Diet had a significant effect on both number of eggs ( $F_{1,31} = 6.50, P = 0.016$ ) and egg mass ( $F_{1,31} = 58.34, P < 0.001$ ).

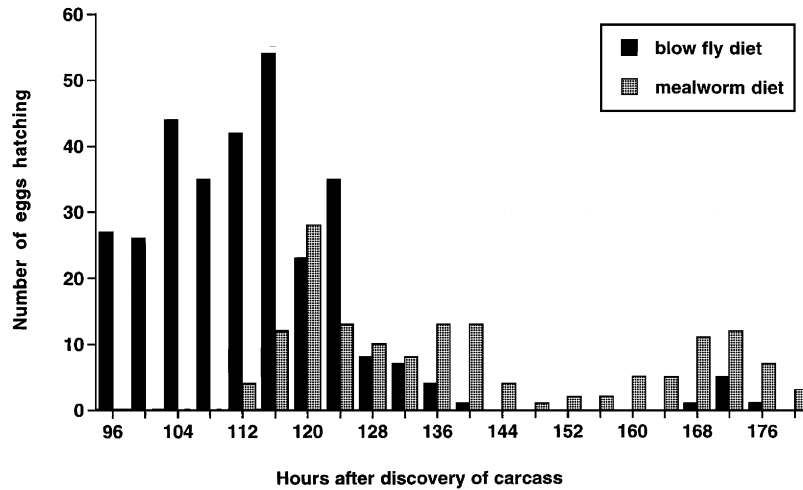


Fig. 2. The number of eggs hatching during each 4 h time interval following discovery of a carcass from *N. orbicollis* females maintained as adults on a diet of mealworm larvae or blowfly larvae. Significance test in text.

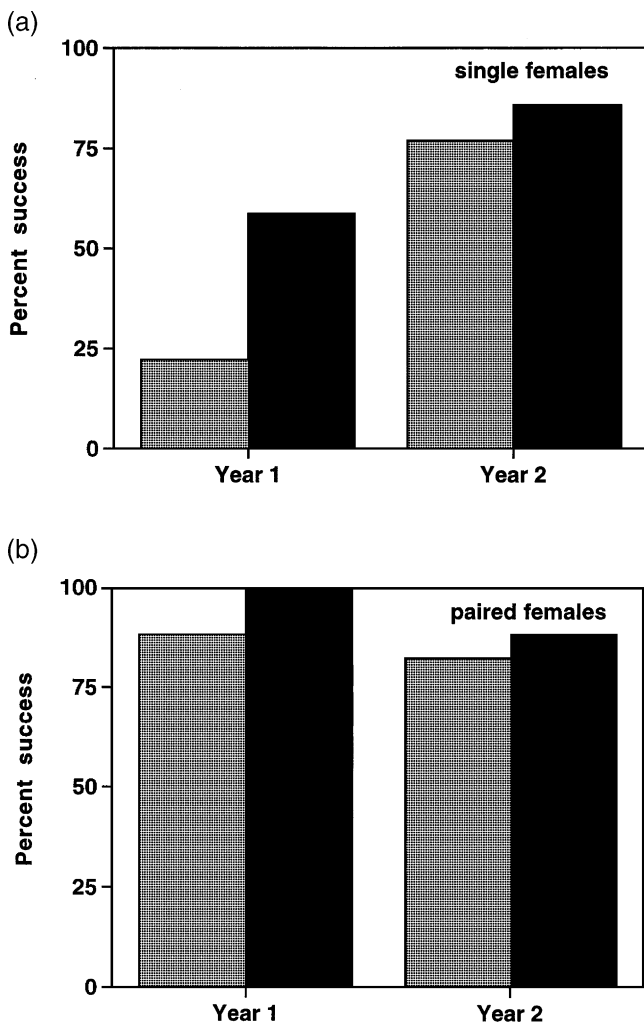


Fig. 3. The percent of control- (gray bars) and JH-treated (solid bars) *N. tomentosus* females producing at least one viable larva (=“success”) in response to discovery of a carcass when breeding alone (a) or paired with a male (b). Wald  $\chi^2$  for single females:  $\chi^2_{\text{YEAR}} = 9.88, P_{\text{YEAR}} < 0.002, \chi^2_{\text{TREATMENT}} = 4.39, P_{\text{TREATMENT}} = 0.036$ ; for paired females:  $\chi^2_{\text{YEAR}} = 1.32, P_{\text{YEAR}} > 0.20, \chi^2_{\text{TREATMENT}} = 1.32, P_{\text{TREATMENT}} > 0.20$ .

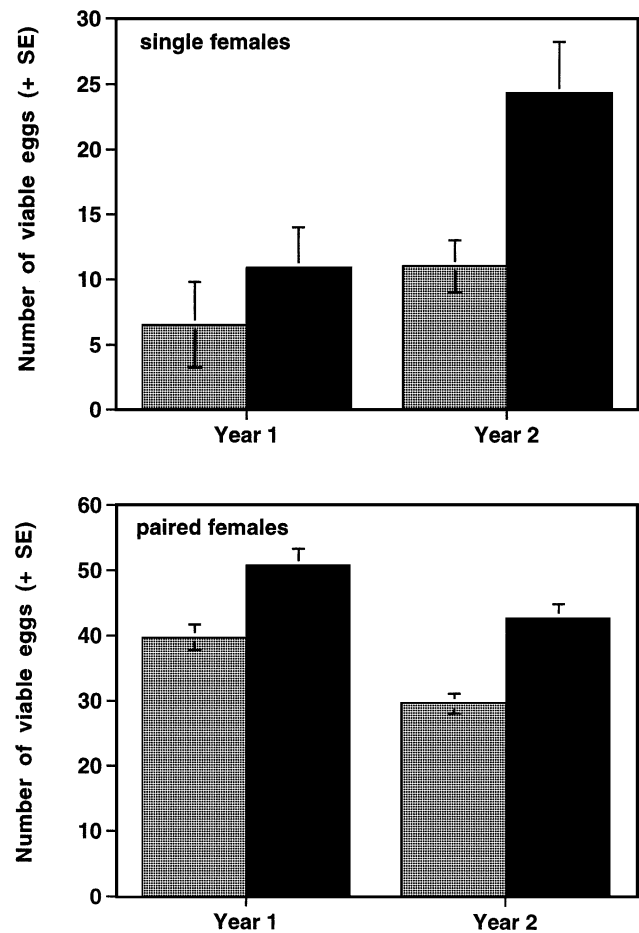


Fig. 4. The mean ( $\pm$ SE) number of viable eggs from control- (gray bars) and JH-treated (solid bars) *N. tomentosus* females when breeding alone (a) or paired with a male (b). ANOVA for single females:  $F_{\text{YEAR}(1,33)} = 8.23, P_{\text{YEAR}} < 0.01, F_{\text{TREATMENT}(1,33)} = 8.39, P_{\text{TREATMENT}} < 0.01$ ; for paired females:  $F_{\text{YEAR}(1,56)} = 5.26, P_{\text{YEAR}} = 0.26, F_{\text{TREATMENT}(1,56)} = 9.20, P_{\text{TREATMENT}} < 0.01$ .

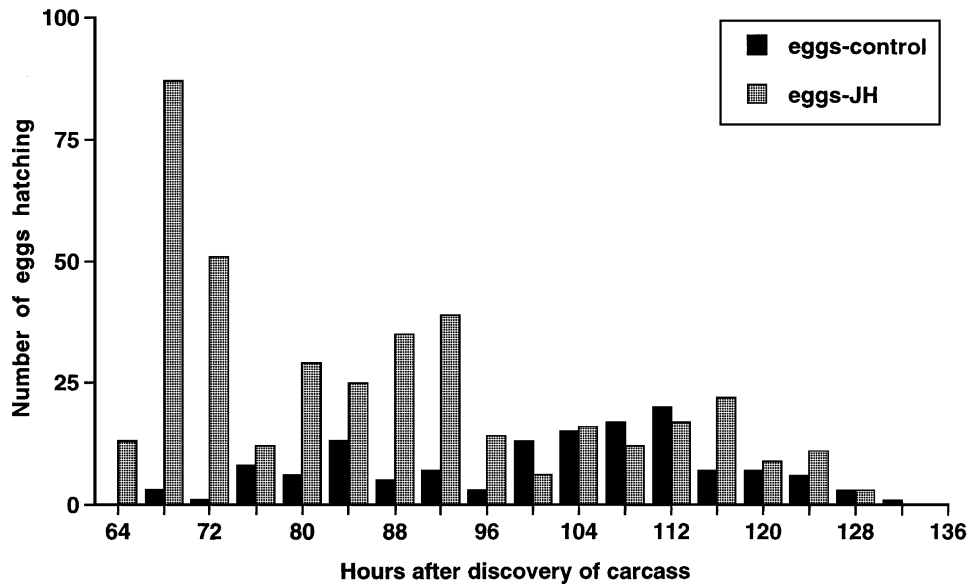


Fig. 5. The number of eggs hatching during each 4 h time interval following discovery of a carcass from control- and JH-treated *N. tomentosus* females breeding alone. Significance test in text.

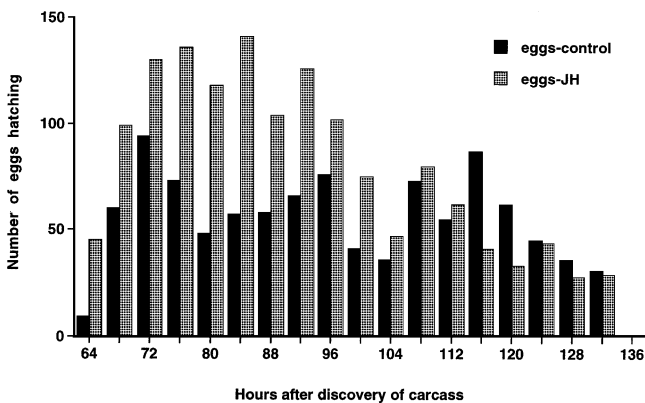


Fig. 6. The number of eggs hatching during each 4 h time interval following discovery of a carcass from control- and JH-treated *N. tomentosus* females breeding in pairs. Significance test in text.

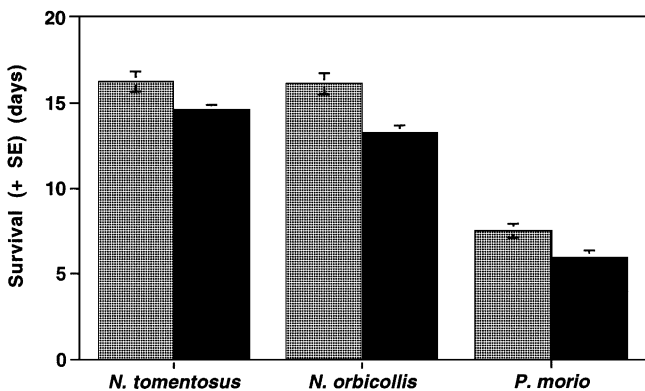


Fig. 7. Mean ( $\pm$ SE) survival in days of control (gray bars) and hormone (solid bars) females when starved. *N. tomentosus* was treated with JH III. *N. orbicollis* and *P. morio* were treated with the JH analog methoprene. Significance tests in text.

pared to controls (Fig. 7,  $P < 0.02$ , Wilcoxon's test). Both body mass rank (ANCOVA,  $F_{1,36} = 23.24$ ,  $P < 0.001$ ) and methoprene treatment ( $F_{1,36} = 6.86$ ,  $P = 0.013$ ) affected survival time in *P. morio*. Survival times under a starvation regime in the laboratory may be longer than in the wild because food was provided in excess until the start of the experiment, and because energetically expensive activities such as flight were suppressed.

#### 4. Discussion

When a female burying beetle discovers a valuable resource suitable for breeding, there is an ecological need to respond quickly. A female of breeding age is unlikely to bypass the rare opportunity of a carcass, even if in a poor nutritional state. We found that undernourished females were constrained in three ways. They produced fewer eggs, eggs were of smaller mass, and it took longer to oviposit compared to well nourished females. It is possible that the smaller egg mass could, in part, account for fewer total eggs hatching, but this is yet to be investigated. A smaller egg mass might also result in a smaller larva that could increase larval mortality or lengthen the period of development. The delay in oviposition (assessed indirectly by time of hatching) can likely be explained by the necessity for adult females to spend time feeding (and subsequent time for incorporation of nutrients into developing oocytes) after discovery of a carcass. Poorly fed but not well-fed females will take time to feed on a fresh carcass prior to oviposition (Trumbo et al., 1995).

Many previous studies of insects, generally using starvation or a severely restricted diet, have found that nutrition affects the number of eggs oviposited (McCaffery, 1975; Wall and Begon, 1987; Karlsson and Wickman, 1990; Moehrlin and Juliano, 1998), the mass of eggs (Murphy et al., 1983; Karlsson and Wickman, 1990) or the latency to oviposition (Ives, 1981; Matura and Morooka, 1983; Weaver, 1984; Whitman, 1986; Rankin et al., 1995b; Moehrlin and Juliano, 1998). Few studies have recorded all three responses (fewer eggs, smaller eggs, delayed oviposition) to poor nutrition. In the present study, we employed an alternative, less preferred diet (mealworm larvae provided in excess) that is commonly used in laboratory studies of burying beetles.

The detrimental effect of poor nutrition on reproductive performance in burying beetles might be related, to some degree, to the lower titers of JH found in poorly nourished females. When JH levels were experimentally increased, independent of nutrition, the number of eggs oviposited and the proportion of females ovipositing quickly were increased. Burying beetle females typically oviposit more eggs than will be reared on a carcass (Wilson and Knollenberg, 1984; Bartlett, 1987; Trumbo, 1990) perhaps as insurance against poor hatching (Bartlett, 1987). The inability of poorly fed females to produce a large clutch may be especially disadvantageous on larger carcasses that can support a female's maximum clutch, and in competitive interactions in which females destroy each other's offspring (Eggert and Müller, 1992; Scott, 1997). Because *N. tomentosus* females in this study were collected in the field, the inter-year variation might have been affected by nutrition prior to trapping or the age of females at the start of the experimental manipulation.

Single females were more likely to attempt reproduction if administered JH. This result suggests that the impact of JH on physiology had behavioral effects. Almost all paired females attempted reproduction so there was little variation in this measurement that could be altered by hormone treatment. The probability that a single female will attempt to breed without a male (utilizing stored sperm) varies across species of *Nicrophorus*. *N. orbicollis* females almost always attempt to breed when alone (Scott and Traniello, 1990; Trumbo, 1991); *N. investigator* females rarely if ever breed without a male (Smith and Heese, 1995). *N. tomentosus* from Connecticut appear to be intermediate. We have found that as *N. tomentosus* females age, they are more likely to attempt to breed without a male (personal observations). The high proportion of single females failing to oviposit in our experiments may have been caused by the relatively young age of these beetles (the experiment began near the start of the breeding season). We suspect that JH treatment overcame the inhibition that some younger females had to initiate breeding alone. Paired females may be less

likely to show an effect of JH supplementation because of their already high probability of breeding. It would be interesting whether JH levels in females unable to locate a carcass gradually increase with age, as the opportunities for breeding before the end of the reproductive season become fewer. It may be that JH supplementation would have less effect on older females.

JH treatment also affected the latency to oviposition in *N. tomentosus*. This effect was significant only for single females. Under the conditions of these experiments, the first larvae to hatch occurred between 64 and 68 h after discovery of a carcass. This was not affected by JH treatment. JH treatment, however, did increase the proportion of broods beginning to hatch during the early 64–68 h time interval. This may indicate that there is a physiological limit to how quickly females begin to oviposit after discovery of a carcass; JH treatment may push more females toward that limit but cannot induce earlier oviposition. It is not surprising, then, that the latency of the reproductive response in single females, which are less likely to initiate breeding than paired females, was more affected by JH treatment.

Given the advantages of responding quickly to a reproductive opportunity in burying beetles, and the positive effect of JH on reproduction, an obvious question is why there has not been selection on females to maintain higher levels of JH while searching for a carcass. Life history theory (Calow, 1979; Finch and Rose, 1995) would lead us to expect that higher titers of hormones involved in reproduction might have negative effects on other components of fitness. In the present study, JH or a JH analog decreased starvation survival in three species (*N. orbicollis*, *N. tomentosus* and *P. morio*). A negative relationship between JH treatment and survival has been demonstrated in a number of insects. Possible mechanisms include (1) less ability to cope with infection (Khafagi and Hegazi, 2001); (2) increased senescence (Tatar et al., 2001); or (3) greater energetic demands. The mechanism by which JH increases mortality in burying beetles was not the focus of the present study. The negative effect of JH over a short period of time in starved beetles does suggest that greater energetic demands might be one source of greater mortality. This is consistent with a Y-model of allocation in which limited resources are shunted toward either reproduction or the soma (Chippindale et al., 1993; Zera and Harshman, 2001). Experimental manipulation of fed individuals, and of individuals on different diets, may provide insight into other mechanisms by which JH affects survival.

In the German cockroach *Blattella germanica* L. and the fruit fly *Drosophila melanogaster* L., lower JH activity is associated with less metabolic activity (Demark and Bennett, 1985; Tatar et al., 2001).

Removal of the corpora allata (the source of JH) in *Labidura riparia* Pallas stops oocyte development and leads to an increase in mass of the fat body (Baehr et al., 1982), a response that would likely enhance resistance to starvation. Allatectomy is known to increase longevity in a number of insects (Tatar and Yin, 2001).

It is also possible that JH affects tradeoffs within the sphere of reproduction. In the ring-legged earwig, JH supplementation early in adult life shortens the time to first oviposition but also results in a smaller clutch (Rankin et al., 1995a). One interpretation is that JH supplementation stimulated young females into reproduction that had not had adequate time to feed and store resources in the fat body. The present study did not examine the effect of JH on egg mass. We have no a priori reason to expect a positive, negative or neutral effect.

The amount of JH topically applied in JH supplementation experiments was fairly high in our study. The large size of the subjects, the naturally high levels of JH as measured by radioimmunoassay (Trumbo et al., 1995), and the production of both positive and negative effects on different components of fitness, consistent with life history theory, leads us to believe the effects were physiological, not pharmacological. Future work employing a dose–response methodology might shed further light on the nature of the response of burying beetles to JH.

We hypothesize that JH mediates the tradeoff between reproductive readiness and starvation survival in burying beetles. During periods of poor nutrition, lower JH titers may increase the chance that a female will survive a period of starvation. We further hypothesize that lower circulating titers of JH constrain the ability of females to produce as many eggs or produce eggs as quickly when encountering a reproductive opportunity. JH may be especially important in competitive interactions at the time reproduction is initiated (Röseler, 1985). We expect that JH will play a significant role in social interactions which vary in burying beetles from aggressive exclusion to communal breeding with joint care of offspring (Eggert and Müller, 1992; Scott and Williams, 1993; Trumbo and Wilson, 1993).

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