

Reproductive rate and longevity in the waterstrider, *Gerris buenoi*

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In this laboratory study, the relationship between egg output and longevity at three food levels is examined in adults of the waterstrider, *Gerris buenoi*. There was no effect of food level on estimated lifetime fecundity. However, egg production rate was halved under low food conditions. This reduction in reproductive rate was balanced by a near doubling of female longevity under food scarcity. Males lived longer than females, but longevity was not significantly related to food level. Egg fertility was not significantly different across treatments. Body size accounted for less than 5% of the variation in all these variables. These data support a central component of life history theory: the assumption that there is a trade off between reproductive rate and longevity.

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On trouvera ici les résultats d'une étude expérimentale sur la relation entre la production d'oeufs et la longévité à trois régimes alimentaires différents chez le patineur, *Gerris buenoi*. La quantité de nourriture reste sans effet sur la fécondité globale estimée. Cependant, le taux de production d'oeufs diminue de moitié lorsque la nourriture est peu abondante. Cette réduction du taux de reproduction est compensée par l'augmentation (2×) de la longévité des femelles dans des conditions de pénurie de nourriture. Les mâles vivent plus longtemps que les femelles, mais leur longévité n'est pas reliée significativement à la quantité de nourriture. La fécondité des oeufs ne varie pas significativement aux divers traitements. La taille du corps explique moins de 5% de la variation de toutes ces variables. Ces résultats confirment un concept important de la théorie démographique : l'existence d'un système de compensation entre le taux de reproduction et la longévité.

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Introduction

Waterstriders feed upon dead or disabled insects trapped upon the water surface, emerging aquatic insects, and other waterstriders. This food resource is highly variable in time and space (Spence 1983; Nummelin 1987) and therefore females probably face times of both food abundance and scarcity. Recent studies suggest that in some field populations, food may limit both larval growth and development (Spence 1986), and reproductive rate of adult females (L. Rowe and G. G. E. Scudder, unpublished).

While there have been several studies of temperature and photoperiod effects on growth, development, wing form, and egg output (Vepsäläinen 1971, 1973, 1974; Jamieson 1973; Spence *et al.* 1980), there have been few studies concerning the effects of food ration on life history traits. Kaitala (1987, 1988), in a study of Finnish gerrids, found that those associated with temporary habitats appeared to balance reproductive output with longevity. *Gerris thoracicus* females maintained with abundant food had high reproductive rates and short life spans, while those with scarce food had low reproductive rates and long life spans.

Negative relationships between reproductive rate and longevity suggest a cost of reproduction. Life history theory assumes that there is a trade off between investment in reproduction early and late in life; therefore, reproductive rate cannot be maximized at all ages (Williams 1966; Reznick 1985; Partridge and Harvey 1985, 1988). This trade off may manifest itself as a negative correlation between reproductive rate and longevity, when reproductive rate is phenotypically manipulated. However, relatively few manipulative studies have been undertaken (Reznick 1985; Partridge and Harvey 1985, 1988). In this

paper, we describe the reproductive responses of adult *Gerris buenoi* when food level is varied.

Materials and methods

The general life history of *Gerris buenoi* in British Columbia has been described earlier (Jamieson 1973; Spence and Scudder 1980; Spence *et al.* 1980; Spence 1983). Macropterous adults of *G. buenoi* which had overwintered, were collected on April 7, 1988 from a pond in the Botanical Gardens at the University of British Columbia. Regular observation in the weeks prior to collection, indicated that adults had not begun breeding and were still rapidly colonizing the pond up to the date of collection. After capture, adults were held for 6 days in an environmental chamber at 10–12°C with a light:dark cycle of 18:6 h.

Beginning on April 13, 15 pairs of males and females were assigned randomly to one of three food level treatments; high (12 flies per day per pair), medium (6 flies per day per pair) and low (3 flies per day per pair); food consisted of frozen fruit flies, *Drosophila melanogaster*. Each pair (five per treatment) was placed in a polyethylene pail (20 cm diam.), filled with dechlorinated water to a height of 5–8 cm. Within each pail was a styrofoam strip ("ovistrip"), approximately 6 cm², which provided a surface for oviposition and a dry resting position. Pails were held in an environmental chamber at 22 ± 1°C with a light:dark cycle of 18:6 h.

Food, ovistrips, and 30–50% of the water were replaced daily and at least once a week 100% of the water was replaced and pails were cleaned. All ovistrips removed on each day were placed in a single pail (25 cm diam.) containing 5–8 cm of dechlorinated water. Four to 5 days after oviposition, eggs on each ovistrip were counted under a microscope (6×) and scored as fertile (tan mottled surface) or infertile. Individuals that died were removed and preserved in alcohol. If only one individual remained in a pail then food ration per pail was cut in half. In the low food treatment, this required alternating the ration between 1 and 2 flies daily. The experiment continued until all individuals in all treatments had died. The cause of mortality was never clear; individuals were usually found floating on the surface and rarely

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underwater. Preserved individuals were dissected to count the number of chorionated eggs remaining in females and whether the wing muscles had undergone histolysis in both sexes.

We measured lifetime reproductive success (total fecundity), the percentage of eggs that were fertile, reproductive rate (total fecundity divided by longevity), and male and female longevity. Unless stated otherwise, one-way analysis of variance was used for all comparisons of parameter means relating to oviposition, across treatments. The Dunn-Sidak method was used to compare individual means. Percent fertility data were log transformed prior to analysis.

Results

Prior to the following analyses, body size (total body length) was calculated as a covariate of each response variable in analyses of covariance. In all cases, body size accounted for less than 5% of the variation.

Figures 1 and 2 present the results of the effect of food on lifetime fecundity, oviposition rate, fertility and longevity. Food level had no significant effect on lifetime fecundity of *G. buenoi* ($F = 1.31$, $p > 0.1$; Fig. 1). However, reproductive rate declined significantly at the low food level ($F = 17.79$, $p < 0.001$; Fig. 1). Reproductive rate was reduced in the low food treatment to approximately 51% of that at high food level, from 4.89 to 2.38 eggs per day. There was a slight and insignificant reduction to 4.81 eggs per day in reproductive rate of females in the medium food treatment. This suggests that our medium food level is very near the level required for maximum egg production. Daily variation in egg production rate was high in all treatments with oviposition ranging from 0 to 18 eggs per day. All females had a postreproductive period, between the last egg laid and the time of death, that varied greatly within treatments, ranging from a few days to a few weeks (no treatment effect, $F = 1.4$, $p > 0.1$).

One female in the medium food treatment never produced a fertile egg. On two occasions, the male of the pair was replaced with a male known to be fertile, for 24 h. In both cases copulation was observed, but no fertile eggs resulted, so the female was evidently infertile. Nevertheless, all other reproductive variables of this female were within the range of other females from the treatment. In the remaining females fertility was relatively high, but quite variable (individual means, 55–98%). There was no significant difference in percent fertility between treatments when the infertile female was excluded from the analysis ($F = 2.394$, $p > 0.1$; Fig. 1). There was a decrease in fertility at the lower food levels. This trend disappears if only data from the first 30 days (when all females are still ovipositing; $F = 0.1$, $p > 0.5$; Fig. 1) are included, suggesting that low fertility may be associated with age of males or females.

Female longevity was significantly increased at low food levels ($F = 22.2$, $p < 0.001$; Fig. 2). Mean longevity almost doubled in the low food treatment relative to the high food treatment, from 46 to 82.6 days. Mean longevity also increased in the medium food level to 53.4 days (28%), but this difference was not significant. On the other hand, male longevity was not affected by treatment ($F = 3.57$, $p = 0.06$; Fig. 2). Variation within treatment was high and the mean longevity of males at the medium food level was less than either high or low food treatments. Mean male longevity was significantly greater than females' within each treatment (separate *t*-tests for each treatment; $p < 0.05$).

Dissection of dead females revealed that histolysis of wing muscles, indicated by their absence, had occurred in all individuals regardless of treatment. All but two individuals had

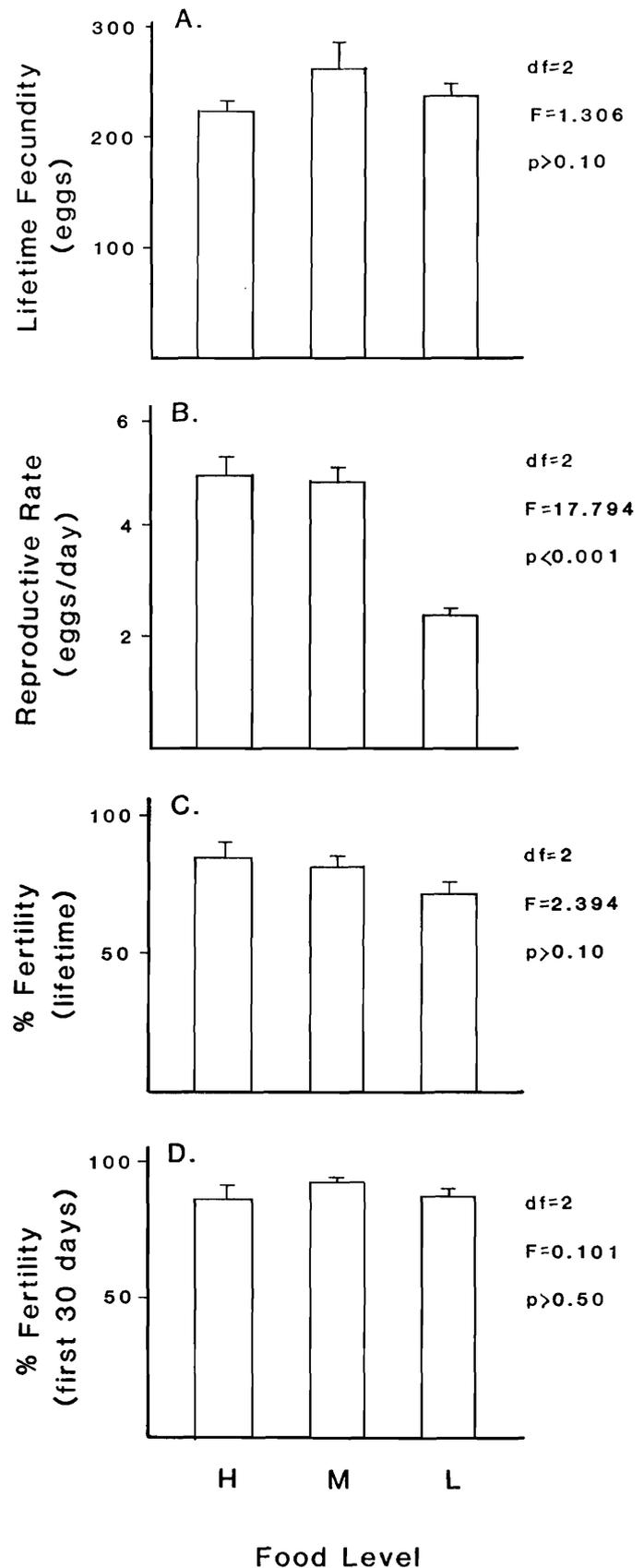


FIG. 1. (A) Mean lifetime fecundity. (B) Mean daily egg output (reproductive rate). (C) Mean percent fertility over the experiment. (D) Mean percent fertility for the first 30 days. Bars represent means (\pm SE) for high (H), medium (M), and low (L) food levels.

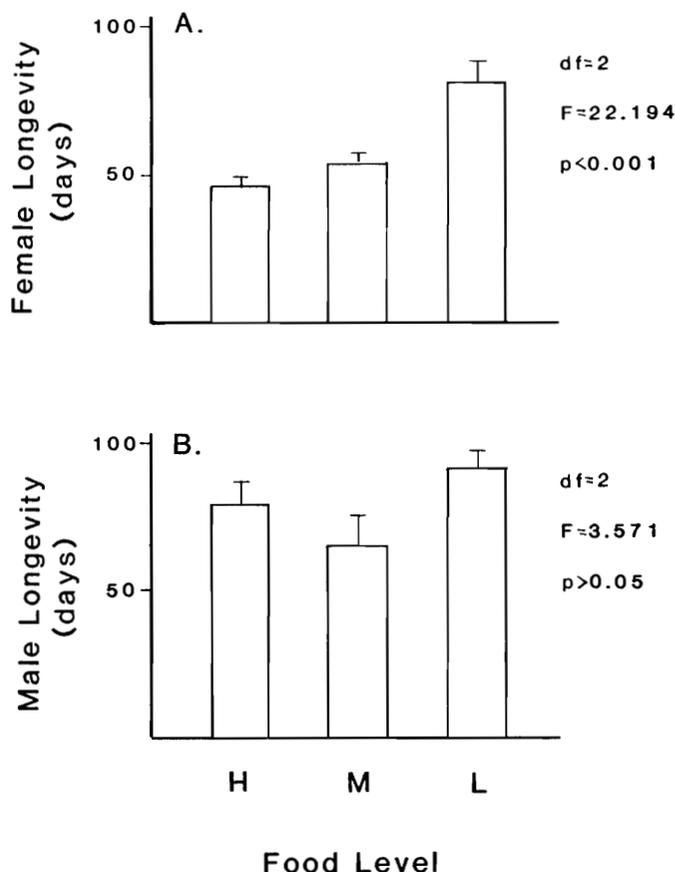


FIG. 2. (A) Mean longevity of females. (B) Mean longevity of males. Bars show means (\pm SE) for high (H), medium (M), and low (L) food levels.

no eggs remaining. Both females with eggs had the lowest lifetime fecundities in their respective treatment groups (high and low food).

Discussion

Reproductive rates of female *Gerris buenoi* are sensitive to laboratory manipulations of food level and there is a negative relationship between reproductive rate and longevity. Despite a 50% reduction of egg production rate under food shortage, lifetime fecundity was unaffected. Females maintained a high total fecundity by doubling their life span. A similar negative relationship between reproductive rate and longevity was reported for *G. thoracicus*, except that total fecundity was also reduced at low food in this species (Kaitala 1987). However, Kaitala (1987) could not address the relationship between reproductive rate and lifetime fecundity since her experimental animals were collected well into the breeding season and thus had probably oviposited a significant portion of eggs prior to the experiment.

Negative relationships between reproductive rate and longevity provide evidence for costs of reproduction, which are assumed in life history theory. The few experimental manipulations of reproductive rate, such as ours, generally reveal negative correlations with longevity (Reznick 1985; Partridge and Harvey 1985, 1988). Although lifetime fecundity was not affected by food levels at the levels used in these experiments, we have found reduced lifetime fecundity in similar experiments when females are maintained at food levels lower than those used here. Presumably, if food level was low enough,

females would produce no eggs and eventually starve. Nonetheless, in all of our experiments with egg-producing females, the negative relationship between reproductive rate and longevity is preserved.

We suspect that our lifetime fecundity estimates closely reflect the potential fecundity of this bug. Our estimates of both lifetime fecundity and reproductive rate when food is abundant are very near to those reported for this species by Spence (1989), and in our own subsequent experiments with bugs that overwintered in the laboratory. However, estimates of total fecundity obtained here probably greatly overestimate mean levels occurring in nature, for several reasons. We used near optimum conditions for the Gerrids. Laboratory temperature (22°C, 24 h) was near the optimum for egg production rate in this species, and this rate declines dramatically below this temperature (Spence *et al.* 1980). During the reproductive period of these spring breeders, temperature often drops below 10°C in the field where egg production of *G. buenoi* ceases (Spence *et al.* 1980). In addition, longevity of the adults in this study was not threatened by predators, cannibals, and abiotic factors such as drowning, all three of which almost certainly conspire to reduce adult Gerrid life spans (Brinkhurst 1966; Maynard 1969; Jamieson 1973; Spence 1983; L. Rowe and G. G. E. Scudder, unpublished).

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Infanticide by female wolves

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Video recordings made inside wolf dens chronicle two episodes of infanticide by different α females within a captive pack of timber wolves (*Canis lupus*). In one instance, infanticidal behaviour was interspersed with maternal behaviour. These cases are discussed in terms of the proximate causes of infanticide. It is also suggested that the killing of pups born to subordinate females by α females may be a common occurrence in both captive and free-ranging wolf packs.

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Des enregistrements sur vidéo à l'intérieur de repaires ont permis d'assister à deux cas d'infanticide par des femelles α au sein d'une meute en captivité de Loups communs (*Canis lupus*). Dans un cas, le comportement infanticide était interrompu par des épisodes de comportement maternel. Les causes immédiates de ces deux cas d'infanticide font l'objet d'une discussion. Il est possible que l'élimination de louveteaux de femelles subordonnées par des femelles α soit un phénomène assez fréquent au sein de meutes de loups en captivité ou en liberté.

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Introduction

Infanticide, the killing of young, has come to be recognized as "a natural and not necessarily pathological behaviour" (Hausfater and Hrdy 1984; p. xi). Along with this change in thinking has come an increased interest in infanticide in wild populations; however, there is still a paucity of data on its frequency of occurrence even for the most studied species (Brooks 1984). This is to be expected since, in the absence of direct observations, infanticidal incidents must be inferred from a number of difficult to determine variables (number of surviving offspring and number of births, pregnancies, or mated females).

For wolves, there are several sources of information relevant to a discussion of infanticidal behaviour and its frequency. In their review of evidence for monogamy in wild wolf packs, Harrington *et al.* (1982) concluded that, where possible (i.e., in packs containing at least two mature females), two or more litters may be born 20–40% of the time. As these figures were based in part on observations of multiple litters that survived long enough to leave the den, and since extra litters probably fail to survive (Packard and Mech 1980), the Harrington *et al.* (1982) estimate is a conservative one.

Other data suggest that the loss of an α female wolf increases the likelihood of multiple litters (Haber 1977, cited in Harrington *et al.*, 1982). It is conceivable that subordinate female wolves may often give birth yet seldom have their pups survive, as is the case with wild dogs (Frame *et al.* 1979). In support of this view,

Altmann (1987) reports that a subordinate female wolf in a captive facility gave birth in 3 successive years despite efforts by the dominant female to prevent her from mating. In none of these years, however, did any of the subordinate female's pups survive. Dominant females have been suspected of killing pups in other captive wolf packs as well (e.g., Klinghammer and Goodmann 1987; Schassburger 1987). Evidence for infanticide in groups of wild carnivores has also implicated dominant females (Lawick 1973; Frame *et al.* 1979; Paquet *et al.* 1982; Packer and Pusey 1984).

Together, these observations suggest that infanticide by dominant females could be a common event in both wild and captive wolf packs. Reports of the behaviour of individuals committing infanticide, however, are absent from the literature. In this study, I present data from two infanticide episodes recorded on video within a captive wolf pack.

Methods

Study site and animals

All observations were made at the Dalhousie Animal Behavior Field Station at Shubenacadie, Nova Scotia. The Shubenacadie pack of timber wolves (*Canis lupus*) were born in captivity at this facility. At the times of the reported incidents, the pack comprised 12 and 9 adult individuals (in 1983 and 1987, respectively).

Den modifications

The three most frequently used dens dug by the wolves within a 3.8-ha enclosure were modified to allow the entire den area to be videotaped using artificial lights and without interfering with the wolves entrance way(s). The wolves showed no signs of being disturbed by the presence of the camera and lights.

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