

## The body size of the New Zealand orb-weaving spider *Waitkera waitakerensis* (Uloboridae) is directly related to temperature and affects fecundity

Brent D. Opell,<sup>a</sup> Andrea M. Berger, and Rachel S. Shaffer

Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, USA

**Abstract.** *Waitkera waitakerensis* occupies lowland forests of New Zealand's North Island, where temperatures decrease in a southwestward direction. The mean annual temperatures of 18 collecting sites, as extracted from GIS data, are directly related to the first femur length of adult females. Neither site elevation nor phylogeny affected spider size or other variables examined. The direct relationship between spider body size and environmental temperature followed a pattern observed in other terrestrial arthropods with a univoltine life cycle and can probably be explained by the longer growing season of warmer regions. Egg diameter was uniform across the species. Site temperature and female first femur length were each directly related to the number of eggs deposited in egg sacs. The date of egg sac collection was inversely related to egg number, suggesting that clutch size declines during the reproductive season. Females deposit eggs beneath a triangular platform and then cover them with a lower silk sheet. The area of this upper platform and the volume of the egg sac were each directly related to egg number, but not to female first femur length. The depth of the lower covering was not related to egg number or to spider first femur length. This suggests that spiders use information about the volume of eggs in their abdomens to construct an egg sac whose volume will accommodate the volume of eggs to be laid and that females do so principally by adjusting the size of the sac's upper triangular platform.

*Additional key words:* clinal variation, egg sac construction

---

Environmental temperature affects the size of many animal species. In endothermic vertebrates, body size is often inversely related to temperature, as a larger body size reduces an animal's surface to volume ratio and favors heat retention (James 1970, 1991; Zink & Remsen 1986; Ashton et al. 2000; Ashton 2002a), a phenomenon known as Bergmann's Rule (Bergmann 1847). Among ectothermic animals, generalizations are more difficult to make (Ashton 2002b; Angilletta & Dunham 2003). For example, 19 of 23 turtle species conform to Bergmann's Rule, whereas 61 of 83 species of lizards and snakes show the converse relationship (Ashton & Feldman 2003). By affecting the length of the growing season and by altering developmental time and rate, temperature can affect adult size in different ways (Blanckenhorn & Demont 2004).

In terrestrial arthropods with univoltine life cycles, larger individuals are often found at the lower latitudes or lower elevations of a species' range (e.g., Schoener & Janzen 1968; Masaki 1978; Mousseau & Roff 1989; Scott & Dingle 1990; Orr 1996), where warmer temperatures provide longer growing seasons that permit individuals to attain larger adult sizes (Mousseau 1997). This end-of-season limitation is more common in larger arthropod species that require longer developmental times (Blanckenhorn & Demont 2004). In many ectothermic vertebrates, cooler temperatures delay maturation, permitting individuals to reach larger adult sizes (Angilletta et al. 2004a,b). Although the growth rate is greater at higher temperatures, elevated temperature may impose energy constraints on growth (Angilletta & Dunham 2003) because growth efficiency decreases with increasing temperature (Atkinson & Sibly 1997).

Selection also shapes the relationship between body size and environmental temperature (Angilletta et al. 2004a,b), as maturation time, body size, survivorship, and fecundity are critical elements of a

---

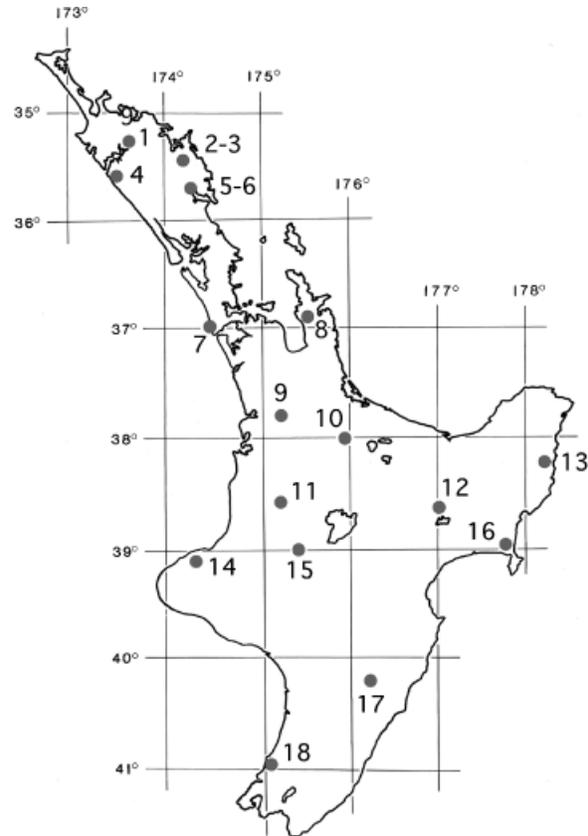
<sup>a</sup> Author for correspondence.

E-mail: bopell@vt.edu

species' life history (Roff 1986, 2002). Increased adult size is of selective advantage because it increases fecundity (Tinkle et al. 1993; Simpson 1995; Hegde & Krishna 1999; Sokolovaska et al. 2000) and contributes to juvenile survivorship (Angilletta et al. 2004a). Larger females tend to produce larger eggs from which larger hatchlings emerge (Williams 1994; Hipfner 2000; Bize et al. 2002; Dzialowski & Sotherland 2004) and these larger hatchlings have greater survivorship (Janzen et al. 2000). However, if a larger adult body size is achieved through longer ontogeny, as is typical of cooler temperatures, these larger individuals must also have lower mortality if their greater size is to be of selective advantage (Stearns 1992; Roff 2002). This is the case in sceloporine lizards, where a Bergmann's cline is explained in part by the higher survivorship of larger individuals that occupy colder regions (Angilletta et al. 2004a) and in odonates, where larger individuals have greater longevity (Sokolovaska et al. 2000).

This study examines the relationships among environmental temperature, body size, and egg size and number in the small, univoltine New Zealand orb-weaving spider *Waitkera waitakerensis* (CHAMBERLAIN 1946). This species is New Zealand's only representative of the family Uloboridae (Opell 1979). It occupies lowland forests (kauri-podocarp hardwood, lowland podocarp hardwood, and lowland hardwood) throughout the North Island, where the mean annual temperature decreases in a southwesterly direction (Fig. 1; Forster 1967; Forster & Forster 1999; Opell 2006). Females have a cephalothorax-abdomen length of 4–5 mm and a mass of 8–9 mg (Opell 1999). They deposit their first triangular, pyramidal egg sacs at the edge of their webs in late December to mid-January (Fig. 2; B.D. Opell, unpubl. data). Egg sacs are left unattended after they are produced and a female continues to construct webs, feed, and produce additional egg sacs for 1–2 months. If the life cycle of this species is like that of other temperate members of the Family Uloboridae, second or third instars remain dormant during the winter, resume growth in the spring, and mature as sixth instars (Berland 1914; Opell 1979, 1982; B.D. Opell & P.E. Cushing, unpubl. data).

We hypothesize that, as in many other arthropods with univoltine life cycles, the size of *W. waitakerensis* is directly related to environmental temperature. If the body size differs across this species, then it should also affect fecundity. Both within species (Wise 1975; Eberhard 1979; Simpson 1995) and between species (Enders 1976; Simpson 1995), comparisons show that spider body size and clutch size are directly related. Simpson (1995) also showed that spider body size is directly related to egg size, although for a given body size, web-



**Fig. 1.** Collecting sites of *Waitkera waitakerensis* listed in Table 1.

building spiders produced smaller eggs than did cursorial spiders. Thus, we also hypothesize that the presumptive larger spiders found in warmer regions produce larger clutches of larger eggs.

We also sought to determine whether *W. waitakerensis* females adjust the volume of their egg sacs to the volume of eggs they deposit, and, if so, how they do so. The orientation and structure of a *W. waitakerensis* egg sac (Fig. 2) makes it clear that females first deposit a dense, triangular silk platform. They next deposit a mass of eggs that stick to one another and to the underside of this platform and then cover the egg mass with a lower silk sheet. Thus, an egg sac's volume could be established by altering either the size of the triangular platform or the size of the lower covering sheet. The first mechanism would require information about the egg volume contained within a spider's abdomen before egg sac construction, whereas the second would require only a response directed by the deposited egg mass. As the latter mechanism appears to be simpler, we hypothesized that a female adjusts the size of her egg sac to clutch size principally by spinning a lower covering that is large enough to contain the egg mass that has been



**Fig. 2.** Egg sacs of *Waitkera waitakerensis* suspended at the edge of an orb web.

deposited. We further hypothesized that the size of the sac's upper triangular platform is directly related to the length of the female's first femur, but that it is not related to the number of eggs within an egg sac.

## Methods

### Collection

The specimens used in this study were collected at 18 sites (Table 1, Fig. 1) in 1991 and 1994 by Brent Opell and in 1996 by Brent Opell and Jason Bond. Some egg sacs were collected with females, whereas others were not associated with females, as sacs accumulate near webs or past web sites where it is not possible to associate them with females unequivocally. This study includes only the more common and widespread forest-dwelling populations of *Waitkera waitakerensis*. The larger, rock-dwelling ecotypes found at four Northland sites (Opell 2006) were excluded because reliable temperature data are not available for these cooler, sheltered microhabitats. Voucher specimens are deposited in Dunedin's Otago Museum and Auckland's Landcare Research collections.

### Measuring spiders and egg sacs

As an index of spider size, we measured the first femur lengths of alcohol-preserved adult female specimens under a dissecting microscope. We opened intact

egg sacs and counted the eggs or spiderlings they contained. From each egg sac that contained eggs, we measured the diameter of four eggs selected at random. We did not measure the diameters of eggs that had developed beyond the early blastodisk stage because eggs begin to elongate after this stage. We measured the three sides of an egg sac's upper triangular platform ( $L_1$ ,  $L_2$ ,  $L_3$ ) and the depth of the egg sac's lower covering sheet ( $H$ ) and used the following formulas to determine platform area and egg sac volume:

$$\begin{aligned} \text{Area of triangular platform (ATP)} \\ &= \sqrt{S(S - L_1)(S - L_2)(S - L_3)} \\ \text{Volume of egg sac} &= (\text{ATP} \times H)/3 \end{aligned}$$

where  $S = (L_1 + L_2 + L_3)/2$ .

### Determining temperature

We extracted the mean annual temperature of each specimen's collecting locality from a GIS data set purchased from New Zealand's National Institute of Water and Atmosphere using the ArcGis program (Environmental Systems Research Institute 2003). These data provide the mean annual temperature for the years 1971–2000 at a spatial resolution of 500 m.

### Additional contributing factors

We examine three additional factors that may affect both body size and egg number and size: phylogeny, collecting bias, and site elevation. A molecular study identified two major clades of *W. waitakerensis*: a northern clade found at localities 1–7 and a central and southern clade found at localities 8–18 (Fig. 1; Opell 2006). Egg sacs from northern localities were sampled throughout the reproductive season, but those from southern localities tended to be sampled later in the season. Consequently, seasonal differences in reproductive fitness may affect patterns in egg number and size. To address this, we assigned sequential collecting days to egg sacs, beginning with the earliest date of December 30 and ending with February 20 (Table 1). Site elevation is not likely to be a contributing factor both because temperature data account for elevation and because *W. waitakerensis* is found principally in lowland habitats. However, to assess the effect of elevation we determined the elevation of each site from topographical maps (Table 1; NZ TopoOnline 2006).

### Statistical analysis

Using the Statistical Analysis System (SAS Institute 1990), we constructed multiple regression models to determine which independent variables contributed

**Table 1.** Collecting sites shown in Fig. 1 and their mean annual temperatures, elevations, and the mean day on which egg sacs were collected, beginning with December 30 as day 1.

Map number	Locality	Latitude (deg.) Longitude (deg.)	°C	Elevation (m)	Mean day
1	Mangamuka Bridge, Omahuta Forest	–35.2273 173.5880	15.118	280	–
2	Raetea State Forest, Lake Omapere	–35.1940 173.4820	14.833	250	24
3	Russell State Forest, Punaruku Road	–35.3799 174.2438	14.548	150	–
4	Waipoua Forest	–35.6164 173.5405	13.507	300	–
5	Whangarei, Coronation Reserve	–35.7303 174.3093	15.361	100	–
6	Whangarei, Reed Memorial Reserve	–35.7071 174.3207	15.053	100	38
7	Karekare, McReady Paddock	–36.9904 174.4675	15.431	150	–
8	Manaia, Mahakirau Reserve	–36.8551 175.6121	14.689	100	48
9	Hamilton	–37.7815 175.2817	14.116	50	30
10	Tukorehe Memorial near Tarukenga	–38.0766 176.1459	12.322	300	34
11	Mapiu, Aratoro Reserve	–38.3295 175.1712	13.669	300	40
12	Te Whaiti	–38.5873 176.7816	11.844	350	40
13	Anaura Bay	–38.2378 178.3298	14.731	100	40
14	Inglewood, Meeting of Waters Reserve	–39.1416 174.1487	12.862	200	24
15	Owhango, Ohinetonga Reserve	–39.8500 174.9314	13.617	450	–
16	Morere Thermal Springs	–38.9838 177.7848	13.746	100	53
17	Dannevirke, Ngapaeruru Reserve	–40.2616 176.2328	12.407	250	–
18	Paekakariki, Kapiti Borough Reserves	–40.9844 174.9441	13.311	150	44

to the dependent variable. We then regressed all possible combinations of the contributing variables ( $p \leq 0.05$ ) and their natural logs, selecting the model that had the greatest  $R^2$  value.

## Results

### Location and temperature

Latitude and elevation, but not longitude, contributed to a model that predicted the mean annual site temperature ( $p = 0.0009$ ,  $R^2 = 0.61$ ;  $p$  for  $\log_N |\text{latitude}|$  and  $\log_N$  elevation: 0.0009 and 0.0244, respec-

tively; temperature =  $67.358 - 13.644 \log_N |\text{latitude}| - 0.760 \log_N$  elevation).

### Temperature and body size

A regression model that included temperature, site elevation, and clade identified temperature as the only predictor of the first femur lengths of all females ( $N = 115$ ) and of the mean femur lengths of females from the 18 sites. In both cases, the model with the greatest  $R^2$  was based on the log values of temperature and femur length. The model based on the mean female first femur length per site (Fig. 3) had an  $R^2$  nearly double that based on all females.

### Egg number and size

A regression model that included temperature, elevation, mean collecting day, and clade identified only temperature and collecting day as predictors of the mean number of eggs in sacs collected from eight sites ( $p = 0.0154$ ,  $R^2 = 0.81$ ;  $p$  for temperature and collecting day 0.0407 and 0.0133, respectively; eggs = 1.398 temperature  $-0.236d + 7.6$ ). Among the 18 females collected with egg sacs, where there was a narrow range of collecting days, only the femur length affected the number of eggs in a sac (Fig. 4).

None of the variables in a regression model that included temperature, elevation, collecting day, and clade predicted egg diameter, which had a mean of  $658 \pm 57 \mu\text{m}$  SE ( $N = 45$ ). There was also no relationship between the first femur lengths of 18 females collected with egg sacs and the diameters of eggs within their sacs ( $p = 0.61$ ).

### Egg sac size

Among the 18 females collected with egg sacs, egg sac volume was not related to first femur length

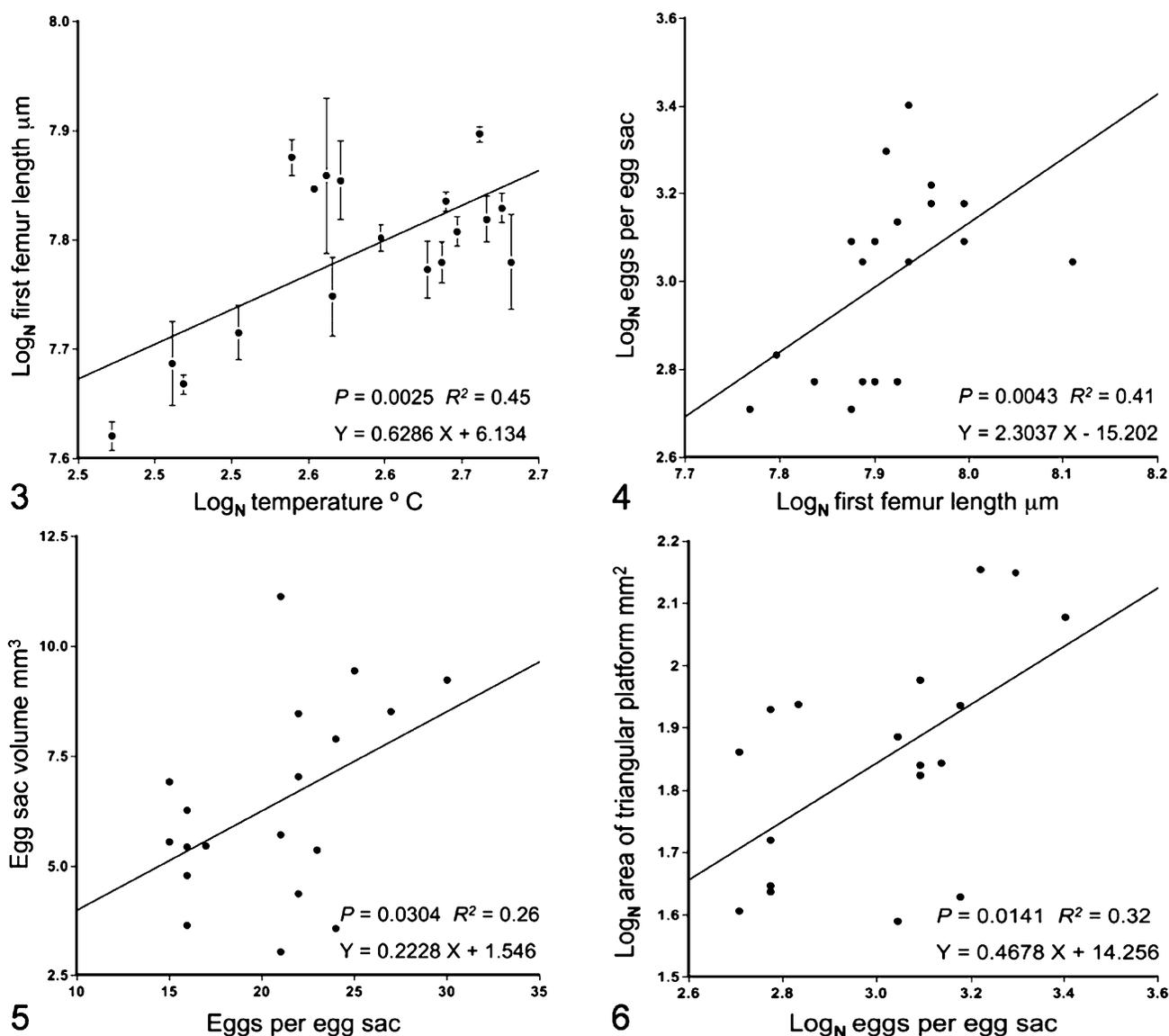


Fig. 3–6. Relationships between: 3. first femur length and temperature, 4. number of eggs per egg sac and first femur length, 5. egg sac volume and the number of eggs per sac, and 6. area of an egg sac's upper triangular platform and the number of eggs in the sac.

( $p = 0.13$ ), but it was related to the number of eggs in the sac (Fig. 5). A regression model that included first femur length and egg number identified only egg number as a predictor of the area of an egg sac's triangular platforms (Fig. 6). Neither first femur length nor egg number was related to the depth of the egg sac's lower covering ( $p = 0.27$  and  $0.43$ , respectively).

### Discussion

As hypothesized, the body size in *Waitkare waitakerensis* females responds positively to temperature, with the largest individuals being found at warmer, northern sites. This pattern is best explained by the longer growing season of these sites that permits individuals to reach larger sizes (Mousseau 1997). Spiderlings may also emerge from egg sacs earlier at warmer sites, develop more rapidly, and attain a larger size before undergoing cold weather diapause. This may both increase over-wintering survival and permit them to mature earlier during the next season.

The hypothesis that spider size and clutch size are correlated was also supported and is consistent with previous studies (Wise 1975; Enders 1976; Eberhard 1979; Simpson 1993; Simpson 1995). As the reproductive season of warmer sites is at least as long as that of cooler regions, this finding indicates that the fecundity in *W. waitakerensis* is directly related to temperature. However, contrary to our hypothesis, and to the generalization that clutch size and egg size are inversely related (Parker & Begon 1986), egg size was uniform across sites. Temperature may impact egg size through dual pathways. Simpson (1995) found that spider body size is directly related to egg size. However, in carabid beetles and cladocerans the number of eggs or juveniles produced increases and the size of the eggs or juveniles decreases as the temperature increases (Yampolsky & Scheiner 1996; Ernsting & Isaaks 2000). These two opposing trends may operate to stabilize egg size in *W. waitakerensis*. The inverse relationship between the number of eggs in a sac and collecting day shows that clutch size declined during the reproductive season, presumably because of declining nutritional resources or female condition.

The number of eggs within a female's abdomen appears to be responsible for directing a female to construct an egg sac of appropriate size for the clutch that she will deposit. This is achieved principally by establishing an upper triangular platform whose size correlates to egg number. There are probably both functional and geometrical explanations for this correlation. An egg sac's triangular platform must be large enough to accommodate the egg mass that will adhere to its lower surface and, as the female hangs

beneath this platform as she deposits eggs, the platform must also be large enough to allow her to maneuver around the growing sphere of eggs. Additionally, the size of the triangular platform has a larger impact on the volume of the egg sac than does the depth of its lower covering. A 50% increase in the length of each side of the egg sac's upper triangular platform results in a 225% increase in egg sac volume, whereas a 50% increase in the egg sac's depth increases its volume by only 150%.

Clinal variation in body size can have a genetic component (Mousseau & Roff 1989; Arnett & Gotelli 1999a) that can be established quickly (Huey et al. 2000). Both the geological history of New Zealand (Suggate 1978; Thornton 1985) and the population structure in *W. waitakerensis* (Opell 2006) suggest that the current distribution of this species involved a southward migration from populations confined to the North Island's warmer Northland region during the Pleistocene. Eruptions of the North Island's Taupo Volcano 20,000 years ago (Thornton 1985) and again ~1855 years ago (Wilson & Walker 1985) formed deep ash fields that extended for hundreds of kilometers over the central and eastern regions of the North Island and probably would have eliminated members of *W. waitakerensis* from these regions. Thus, the size cline observed in *W. waitakerensis* may have been established recently as the species colonized or recolonized regions that have cooler mean annual temperatures.

**Acknowledgments.** Comments by two anonymous reviewers helped improve this article. Collecting permits from New Zealand's Department of Conservation, the Auckland Regional Council Parks Committee, and the Works and Services Department of the Whangarei District Council facilitated this study. Peter Sforza helped extract GIS data. Denis Gibbs introduced me to *Waitkera waitakerensis* and extended hospitality on each of my visits. This study was supported by National Science Foundation grants BSR-8917935 and IBN-9417803 and a National Geographic Society research grant.

### References

- Angilletta MJ & Dunham AE 2003. The temperature-size rule in ectotherms: simple evolutionary explanations may not be general. *Am. Nat.* 162: 332–342.
- Angilletta MJ, Niewiarowski PH, Dunham AE, Leaché AD, & Porter WP 2004a. Bergmann's clines in ectotherms: illustrating a life-history perspective in sceloporine lizards. *Am. Nat.* 164: E-168–E-183.
- Angilletta MJ, Steury TD, & Sears MW 2004b. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life history puzzle. *Integr. Comp. Biol.* 44: 498–509.

- Arnett AE & Gotelli NJ 1999a. Bergmann's rule in the ant lion *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae): geographic variation in body size and heterozygosity. *J. Biogeogr.* 26: 275–283.
- 1999b. Geographic variation in life-history traits of the ant lion, *Myrmeleon immaculatus*: evolutionary implications of Bergmann's rule. *Evolution* 53: 1180–1188.
- Ashton KG 2002a. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecol. Biogeogr.* 11: 505–524.
- 2002b. Do amphibians follow Bergmann's rule? *Can. J. Zool.* 80: 708–716.
- Ashton KG & Feldman CR 2003. Bergmann's rule in non-avian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57: 1151–1163.
- Ashton KG, Tracy MC, & de Queiroz A 2000. Is Bergmann's rule valid for mammals? *Am. Nat.* 156: 390–415.
- Atkinson D & Sibly RM 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.* 12: 235–239.
- Bergmann C 1847. Über die Verhältnisse der Wärmeökonomie der Tiere zu ihrer Grösse. *Gotting. Stud.* 1: 595–708.
- Berland J 1914. Note sur le cycle vital d'une Araignée cribellate, *Uloborus plumipes* Lucas. *Arch. Zool. Expér.* 54: 45–57.
- Bize P, Roulin A, & Richner H 2002. Covariation between egg size and rearing condition determines offspring quality: an experiment with the alpine swift. *Oecologia* 132: 231–234.
- Blanckenhorn WU & Demont M 2004. Bergmann and converse Bergmann latitudinal clines in Arthropods: two ends of a continuum? *Integr. Comp. Biol.* 44: 413–424.
- Chamberlain G 1946. Revision of the Araneae of New Zealand. *Rec. Auckland Inst. Mus.* 3 (Part 2): 85–97.
- Dzialowski EM & Sotherland PR 2004. Maternal effects of egg size on emu *Dromaius novaehollandiae* egg composition and hatchling phenotype. *J. Exp. Biol.* 207: 597–606.
- Eberhard WG 1979. Rates of egg production by tropical spiders in the field. *Biotropica* 11: 292–300.
- Enders F 1976. Clutch size related to hunting manner of spider species. *Ann. Ent. Soc. Am.* 69: 991–998.
- Environmental Systems Research Institute 2003. ArcGIS 8.3. Redlands, CA.
- Ernsting G & Isaaks A 2000. Ectotherms, temperature, and trade-offs: size and number of eggs in a carabid beetle. *Am. Nat.* 155: 804–813.
- Forster RR 1967. The spiders of New Zealand. *Otago Mus. Bull.* 1 (Part 1): 7–124.
- Forster RR & Forster L 1999. Spiders of New Zealand and their Worldwide Kin. University of Otago Press, Dunedin. 270 pp.
- Hegde SN & Krishna MS 1999. Body size and fitness characters in *Drosophila malerkotliana*. *Curr. Sci.* 77: 178.
- Hipfner JM 2000. The effect of egg size on post-hatching development in the Razorbill: an experimental study. *J. Avian Biol.* 31: 112–118.
- Huey RB, Gilchrist GW, Carlson ML, Berrigan D, & Serra L 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science* 287: 308–309.
- James FC 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51: 365–390.
- 1991. Complementary descriptive and experimental studies of clinal variation in birds. *Am. Zool.* 31: 694–706.
- Janzen FJ, Tucker JK, & Paukstis GL 2000. Experimental analysis of an early life-history stage: selection on size of hatchling turtles. *Ecology* 81: 2290–2304.
- Masaki S 1978. Seasonal and latitudinal adaptations in the life cycles of crickets. In: *Evolution of Insect Migration and Diapause*. Dingle H, ed., pp. 72–100. Springer-Verlag, New York.
- Mousseau TA 1997. Ectotherms follow the converse to Bergman's rule. *Evolution* 51: 630–632.
- Mousseau TA & Roff DA 1989. Adaptation to seasonality in a cricket: patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. *Evolution* 43: 1483–1496.
- NZ TopoOnline (accessed May 2006). <http://www.nztopoonline.linz.gov.nz/>
- Opell BD 1979. Revision of the genera and tropical American species of the spider family Uloboridae. *Bull. Mus. Comp. Zool.* 14: 433–549.
- 1982. Cribellum, calamistrum, and ventral comb ontogeny in *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). *Bull. Br. Arachnol. Soc.* 5: 338–343.
- 1999. Changes in spinning anatomy and thread stickiness associated with the origin of orb-weaving spiders. *Biol. J. Linn. Soc.* 68: 593–612.
- 2006. Molecular phylogenetic evidence for the parallel evolution of rock ecomorphs in the New Zealand orb-weaving spider *Waitkera waitakerensis* (Family Uloboridae). *J. Arachnol.* 34: 467–475.
- Orr MR 1996. Life history adaptations and reproductive isolation in a grasshopper hybrid zone. *Evolution* 50: 704–716.
- Parker GA & Begon M 1986. Optimal egg size and clutch size: effects of environmental and maternal phenotype. *Am. Nat.* 128: 573–592.
- Roff DA 1986. Predicting body size with life history models. *BioScience* 36: 316–323.
- 2002. *Life History Evolution*. Sinauer Association Inc., Sunderland, MA. 527 pp.
- SAS Institute 1990. *SAS Users Guide: Statistics*, 6 ed. SAS Institute Inc., Cary, NC.
- Schoener TW & Janzen DH 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. *Am. Nat.* 102: 207–224.
- Scott SM & Dingle H 1990. Developmental programs and adaptive syndromes in insect life-cycles. In: *Insect Life Cycles: Genetics, Evolution and Co-Ordination*. Gilbert F, ed., pp. 69–85. Springer-Verlag, New York.

- Simpson MR 1995. Covariation of spider egg and clutch size: the influence of foraging and parental care. *Ecology* 76: 795–800.
- Sokolovaska N, Lowe R, & Johansson F 2000. Fitness and body size in mature odonates. *Ecol. Entomol.* 25: 239–248.
- Stearns SC 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford, UK. 248 pp.
- Suggate RP 1978. *The Geology of New Zealand*, Vols. 1 and 2. E. C. Keating, Government Printer, Wellington, New Zealand. 820 pp.
- Thornton J 1985. *New Zealand Geology*. Reed Books, Auckland, New Zealand. 270 pp.
- Tinkle DW, Dunham AE, & Congdon JD 1993. Life history and demographic variation in the lizard *Sceloporus graciosus*: a long term study. *Ecology* 74: 2413–2429.
- Williams TD 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biol. Rev.* 68: 35–59.
- Wilson CS & Walker CPL 1985. The Taupo eruption, New Zealand. I. General aspects. *Philos. Trans. R. Soc. London A* 314: 199–228.
- Wise D 1975. Food limitations of the spider *Linyphia marginata*: experimental field studies. *Ecology* 56: 637–646.
- Yampolsky L & Scheiner SM 1996. Why larger offspring at lower temperatures? A demographic approach. *Am. Nat.* 147: 86–100.
- Zink RM & Remsen JV 1986. Evolutionary processes and patterns of geographic variation in birds. In: *Current Ornithology*, Vol. 4. Johnson RF, ed., pp. 1–69. Plenum Press, New York.