SHORT COMMUNICATION

Reproductive strategy of a cave-living arachnid with indeterminate growth
(*Phrynus longipes*; Amblypygi: Phrynidae)

Kenneth James Chapin and **Emily Katherine Chen**:   Department of Ecology & Evolutionary Biology, University of California, Los Angeles, 612 Charles E. Young Drive East, Los Angeles, CA 90095-7246; E-mail: chapinkj@gmail.com.

Abstract.   Natural selection predicts that organisms should maximize reproductive fitness by exhibiting a tradeoff between the quantity and quality of offspring. While many species clearly show this tradeoff, it is not a ubiquitous phenomenon. Indeed, observing this tradeoff in different organisms is contingent on life history traits, reproductive strategy, parental investment, and physiological constraints. We tested for a tradeoff between the number and quality of offspring in the amblypygid *Phrynus longipes* (Pocock, 1894)—a long-lived, iteroparous arachnid with indeterminate growth, post-ultimate molts, and parental care. We measured the size of gravid females and the mass and number of eggs in their clutches. Egg count, but not mass, was predicted by female size, indicating that we did not detect an offspring quantity-quality tradeoff. We posit that larger female *P. longipes* are laying more eggs rather than increasing investment in each egg. This study is the first of its kind in any amblypygid species.

Keywords: Amblypygid, egg, parental investment, reproduction, reproductive tradeoff

Natural selection predicts that organisms should maximize reproductive fitness by optimizing the tradeoff between the quantity and quality of offspring (Lack 1947, 1954; Smith & Fretwell 1974). This was intuitively posited because organisms have limited resources available in the environment with which to produce offspring. Thus, increasing the quantity of offspring decreases the investment available for each offspring. This tradeoff between quantity and quality has resulted in different reproductive strategies, e.g., r- and K-selection (Pianka 1970). Here, we test for a tradeoff between offspring quality and quantity in the amblypygid *Phrynus longipes* (Pocock, 1894).

Species of the order Amblypygi (Arachnida) have a unique combination of life history traits that provide no clear intuition about the likelihood of exhibiting a tradeoff. Unlike nearly all other arthropods, amblypygids have indeterminate growth and continue to molt after sexual maturity (Weygoldt 2000; Chapin & Hebets 2016). Thus, unlike most other arthropods, amblypygid initial egg size is unlikely to determine final adult size (Smith 1997). Many arthropods with indeterminate growth produce higher quality offspring as they age (Fox & Czesak 2000). For example, older female water fleas (order: Cladocera) with indeterminant growth produce eggs that are larger than the optimal size (Bell 1983; Boersma 1997). Amblypygids are long-lived (perhaps 7–10 years), iteroparous, and produce 10–90 eggs per clutch (Fig. 1; Chapin & Hebets 2016). Amblypygids exhibit high parental care relative to arthropods that typically exhibit a quantity-quality tradeoff (Chapin & Hebets 2016). Females carry the eggsac on the ventral opisthosoma (Fig. 1a). After hatching, young emerge and climb onto the back of the female where they molt before becoming free-living (Figs. 1b,c; Weygoldt 2000; Chapin & Hebets 2016). Thus, amblypygids provide postembryonic parental investment that may limit clutch size and obscure the quantity-quality tradeoff (Boyce & Perrins 1987; Oksanen et al. 2001; Gilbert & Manica 2010; but see Walker et al. 2008). Evolutionary history also provides no clear hypothesis for a tradeoff occurring in *P. longipes*; the closely related Araneae tend to not show the tradeoff, but scorpions do (Killebrew & Ford 1985; Marshall & Gittleman 1994; Brown 2003; Skow & Jakob 2003), and the phenomenon is common among other arthropod groups (Berrigan 1991; Fox & Czesak 2000).

The tradeoff is often detected in semelparous species that exhibit low parental care and use larval-acquired resources to produce eggs (Ford & Seigel 1989; Fox & Czesak 2000). However, the tradeoff is often not detected in taxa with iteroparity and parental care as these factors complicate life history and obscure existing tradeoffs (Gilbert & Manica 2010). In addition, the quantity-quality tradeoff is more obvious in oviparous species, which, unlike viviparous species, allocate a discrete amount of resources to offspring upon or soon after fertilization (Ford & Seigel 1989; King 1993). Egg-laying animals provide finite resources to developing young, which should emphasize energetic constraints on offspring number and quality (Parker & Begon 1986). Spider egg mass scales geometrically with egg diameter and spider eggs have constant energy density (Anderson 1990). We assume the same is true for whip spiders, such that larger eggs require greater energy investment, but often have higher survivability. Larger eggs experience lower rates of desiccation (Anderson 1990; Sota & Mogi 1992). In addition, progeny that arise from larger eggs have better feeding performance (Walker et al. 2003) and may be less resistant to starvation (Gliwicz & Guisande 1992; Wallin et al. 1992). Thus, we tested whether the amblypygid, *Phrynus longipes*, exhibits a tradeoff between the quality and quantity of offspring, with the goal of expanding our understanding of variation in parental investment across arthropods.

We collected twenty-four egg-carrying *Phrynus longipes* from Cueva Matos (*ca.* 18.38°N, 66.68°), Arecibo, Puerto Rico in August 2014. We measured the maximum prosoma width of each female using digital calipers to the nearest 0.1 mm ± 0.1 mm. The prosoma shows allometric growth throughout the life of amblypygids and correlates well with body mass (Chapin 2011; Chapin & Hebets 2016). We stored specimens in 95% ethanol and shipped them to our laboratory at UCLA for further analysis. We recorded the total number of eggs per female and dry mass of eggs from each clutch. We placed individual eggs in microcentrifuge tubes and dried them in a drying oven at 60°C for 120 h. We weighed dried eggs with a microbalance scale to the nearest 1 μg ± 1μg (Orion Cahn C-33). Further, we determined the developmental stage of each egg, and if the embryo was developing.

We compared generalized linear models (GLM) of egg mass predicting egg count with female size as a covariate using Akaike's information criterion corrected for small sample size (AICc) and Akaike's weights (w_i; Burnham et al. 2011; Symonds & Mousalli 2011). We used post hoc linear regressions to examine the relationship between mean egg mass, total egg count, and female size separately.
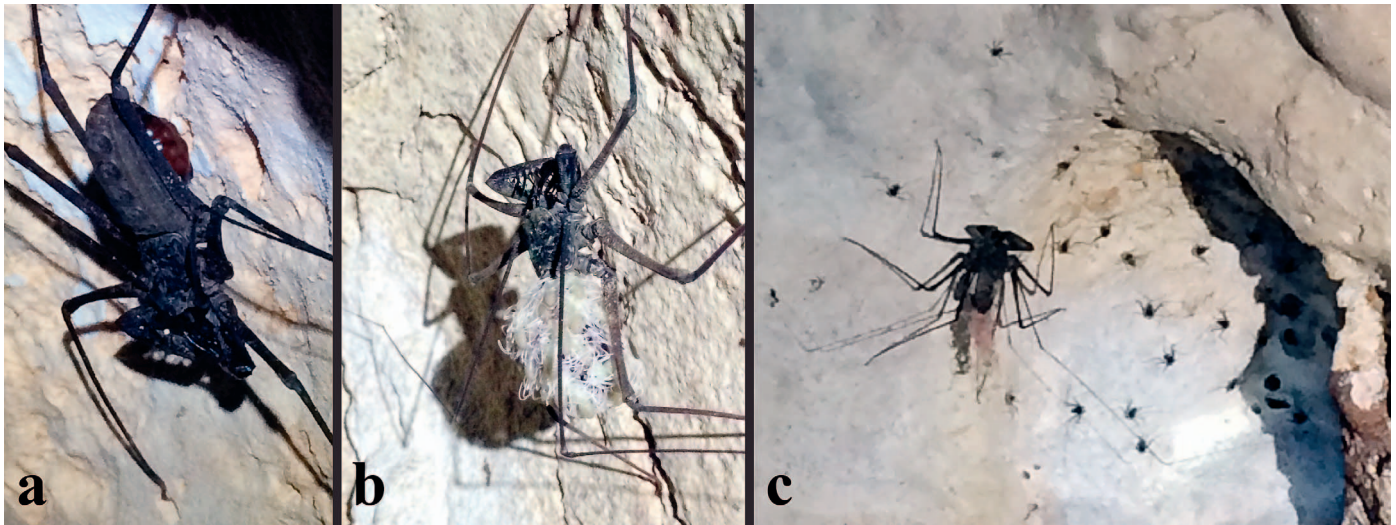
Figure 1.—*Phrynus longipes* (a) with an egg clutch attached to the ventral opisthosoma (b) with offspring on the dorsum and (c) with free-living offspring.

Phrynus longipes had a clutch size of 67 ± 3.3 eggs ($\bar{x} \pm s$; range: 29–94; $n = 24$ clutches). Overall, eggs mass was 4.01 ± 0.12 mg (Range: 3.10–5.21 mg) and the prosoma width of females was 15.80 ± 0.36 mm (range: 12.3–18.9 mm). The best GLM predicting egg count included only female size, not mass (Table 1; estimate ± s = 5.806 ± 1.473, $t_{23} = 3.940$, $P < 0.001$). Larger females (measured as prosoma width) laid more eggs per clutch (adjusted $r^2 = 0.435$, $F_{1, 21} = 17.96$, $P < 0.001$; Fig. 2a) but female prosoma width failed to predict egg mass (adjusted $r^2 = 0.012$, $F_{1, 21} = 1.268$, $P = 0.273$; Fig. 2b). Egg developmental stage or the proportion of embryos that developed did not improve model results.

We did not detect a quality-quantity tradeoff in *P. longipes* (Fig. 2). Larger females had a higher number of eggs but not lower quality offspring, measured as egg mass. Larger females invest more resources into producing more eggs rather than investing more into each egg. Our results support the findings of Fox and Czesak (2000): species that do not show a quantity-quality tradeoff are often iteroparous, use adult-acquired resources for reproduction, or provide postembryonic parental care, all of which are characteristics of *P. longipes* (Fox & Czesak 2000).

Our results generally align with patterns seen in Araneae with few differences that can be attributed to life-history (Killebrew & Ford 1985; Marshall & Gittleman 1994; Brown et al. 2003; Skow & Jakob 2003; Barrantes 2015). Larger, and therefore older, *P. longipes* females laid larger clutches. This is the opposite pattern seen in many arthropods, including Araneae, which lay smaller successive clutches with age (Marshall & Gittleman 1994; Fox & Czesak 2000; Brown et al. 2003). Female Araneae generally lay only a few clutches in their lifetime while female amblypygids can generally produce one to three clutches a year over their lifetime of perhaps as many as 10 years (Weygoldt 2000; Chapin & Hebets 2016). Clutches are expected to become smaller with age in arthropods that acquire resources as larva

Table 1.—Multimodel comparisons of generalized linear models predicting egg count ($n = 24$) in clutches of *Phrynus longipes*. The full model includes egg mass, female size, and their interaction as predictor variables. Female size, but not mass, best predicted egg count.

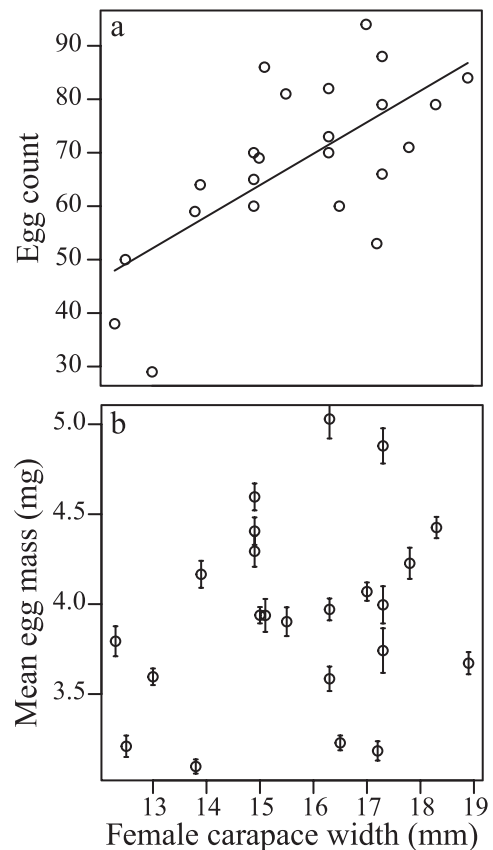| Model	AICc	k	ΔAICc	w_i
mass × size	199.12	4	0.00	0.06
mass + size	196.22	3	−2.90	0.26
size	194.33	2	−4.80	0.67
mass	204.93	2	5.81	< 0.001
intercept only	204.76	1	5.63	< 0.001

Figure 2.—Plots of egg clutch and female measurements for *Phrynus longipes*: (a) Total egg count per clutch predicted by female carapace width (adjusted $r^2 = 0.44$, $F_{1,21} = 17.96$, $P < 0.001$). (b) Mean egg mass predicted by female carapace width (adjusted $r^2 = 0.01$, $F_{1,21} = 1.27$, $P = 0.273$).

and deplete reserves with age (Wasserman & Asami 1985; Boggs 1986; Fox 1993) or where short or variable lifespans make future reproduction uncertain. *Phrynus longipes*, however, has a long lifespan and survivorship probabilities likely increase with age.

Amblypygids exhibit indeterminate growth and continue to molt after maturity. Many arthropods with indeterminate growth produce higher quality offspring as they age (Bell 1983; Boersma 1997; Fox & Czesak 2000;). Surprisingly, older, larger female *P. longipes* produce more but not larger eggs. Amblypygi eggs might already be of an optimal size, such that provisioning resources to eggs might not benefit offspring. Instead, amblypygids invest in a great number of offspring.

Our cave study site provides exceptionally high levels of prey, so we assumed there would be low variation in resource acquisition (Chapin 2015; Chapin & Hill-Lindsay 2016). This is important, because variation in resource acquisition can obscure a tradeoff between size and quantity (van Noordwijk & de Jong 1986). For example, resource scarcity results in unequal rates of resource acquisition and investment in clutches among female conspecifics which may conceal an existing tradeoff (van Noordwijk & de Jong 1986). Intraspecific experiments indicated a tradeoff under high, but not low, resources abundance (Brown 2003). Variable resource acquisition, however, can mask these effects. Despite this, no tradeoff was detected in *P. longipes* between egg size and quantity. Although females are unlikely to be limited by resource acquisition, other factors could potentially prevent a tradeoff from being detected.

Future research should quantify how egg mass impacts survivorship and reproductive fitness. For example, egg size may be influenced by physiological constraints on eggs, including oxygen absorption, nutritional accessibility, and desiccation. Further investigation into factors influencing egg size in amblypygids will provide insight into the diversity of parental investment in arthropods and reveal the unique life history of amblypygids.

ACKNOWLEDGMENTS

LITERATURE CITED

Anderson, J.F. 1990. The size of spider eggs and estimates of their energy content. Journal of Arachnology 18:73–78.

Barrantes, G. 2015. Effect of body size and maternal care on clutch size and egg size in theridoids. Boletin de la Sociedad zoological del Uruguay 24:81–90.

Bell, G. 1983. Measuring the cost of reproduction. III. The correlation structure of the early life history of *Daphnia pulex*. Oecologia 60:378–383.

Berrigan, D. 1991. The allometry of egg size and number in insects. Oikos 60:313–321.

Boersma, M. 1997. Offspring size and parental fitness in *Daphnia magna*. Evolutionary Ecology 11:439–450.

Boggs, C.L. 1986. Reproductive strategies of female butterflies: variation in and constraints on fecundity. Ecological Entomology 11:7–15.

Boyce, M.S. & C.M. Perrins. 1987. Optimizing great tit clutch size in a fluctuating environment. Ecology 68:142–153.

Brown, C.A. 2003. Offspring size-number trade-off in scorpions: an empirical test of the Van Noordwijk and de Jung Model. Evolution 57:2184–2190.

Brown, C.A., B.M. Sanford & R.R. Swerdon. 2003. Clutch size and offspring size in the wolf spider *Pirata sedentarius* (Araneae, Lycosidae). Journal of Arachnology 31:285–296.

*Burnham, K.P., D.R. Anderson & K.P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology & Sociobiology 65:23–35.

Chapin, K.J. 2011. Ecology and natural history of the tree-inhabiting social amblypygid *Heterophrynus batesii* (Butler 1873; Amblypygi: Phrynidae) in eastern Amazonian Ecuador MS Thesis, West Texas A&M University, Canyon, Texas.

Chapin, K.J. 2015. Cave-epigean behavioral variation of the whip spider *Phrynus longipes* (Arachnida: Amblypygi) evidenced by activity, vigilance, and aggression. Journal of Arachnology 43:214–219.

Chapin, K.J. & E.A. Hebets. 2016. Behavioral ecology of amblypygids. Journal of Arachnology 44:1–14.

Chapin, K.J. & S. Hill-Lindsay. 2016. Territoriality evidenced by asymmetric intruder-holder motivation in an amblypygid. Behavioural Processes 122:110–115.

Ford, N.B. & R.A. Seigel. 1989. Relationships among body size, clutch size, and egg size in three species of oviparous snakes. Herpetologica 45:75–83.

Fox, C.W. 1993. The influence of maternal age and mating frequency on egg size and offspring performance in *Callosobruchus maculatus* (Coleoptera: Bruchidae). Oecologia 96:139–146.

Fox, C.W. & M.E. Czesak. 2000. Evolutionary ecology of progeny size in arthropods. Annual Review of Entomology 45:341–369.

Gilbert, J.D.J. & Manica A. 2010. Parental care trade-offs and life-history relationships in insects. American Naturalist 176:212–226.

Gliwicz, Z.M. & C. Guisande. 1992. Family planning in *Daphnia*: resistance to starvation in offspring born to mothers grown at different food levels. Oecologia 91:463–467.

Killebrew, D.W. & N.B. Ford. 1985. Reproductive tactics and female body size in green lynx spider, *Peucetia viridans* (Araneae, Oxyopidae). Journal of Arachnology 13:375–382.

King, R.B. 1993. Determinants of offspring number and size in the brown snake, *Storeria dekayi*. Journal of Herpetology 27:175–185.

Lack, D. 1947. The significance of clutch size. Ibis 89:302–352.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford University Press, Oxford.

Marshall, S.D. & J.L. Gittleman. 1994. Clutch size in spiders: is more better? Functional Ecology 8:118–124.

Oksanen, T.A., P. Jonsson, E. Koskela & T. Mappes. 2001. Optimal allocation of reproductive effort: manipulation of offspring number and size in the bank vole. Proceedings of the Royal Society of London B: Biological Sciences 268:661–666.

Parker, G.A. & M. Begon. 1986. Optimal egg size and clutch size: effects of environment and maternal phenotype. American Naturalist 128:573–592.

Pianka, E.R. 1970. On r- and K-Selection. American Naturalist 104:592–597.Skow, C.D. & E.M. Jakob. 2003. Effects of maternal body size on clutch size and egg weight in a pholcid spider (*Holocnemus pluchei*). Journal of Arachnology 31:305–308.

Smith, C.C. & S.D. Fretwell. 1974. The optimal balance between size and number of offspring. American Naturalist 108:499–506.

Smith, R.L. 1997. Evolution of paternal care in the giant water bugs (Heteroptera: Belostomatidae). Pp. 116–149. *In* The Evolution of Social Behaviour in Insects and Arachnids. (J.C. Cloe, B.J. Crespi, eds). Cambridge University Press, Cambridge.

Sota, T. & M. Mogi. 1992. Interspecific variation in desiccation

survival time of *Aedes* (*Stegomyia*) mosquito eggs is correlated with habitat and egg size. Oecologia 90:353–358.

Symonds, M.R.E. & A. Mousalli. 2011. A brief guide to model selection, multimodel inference, and model averaging in behavioral ecology using Akaike's information criterion. Behavioral Ecology & Sociobiology 65:13–21.

van Noordwijk, A.J. & G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.

Walker, R.S., M. Gurven, O. Burger & M.J. Hamilton. 2008. The trade-off between number and size of offspring in humans and other primates. Proceedings of the Royal Society of London B: Biological Sciences 275:827–834.

Walker S.E., A.L. Rypstra & S.D. Marshall. 2003. The relationship between offspring size and performance in the wolf spider *Hogna helluo* (Araneae: Lycosidae). Evolutionary Ecology Research 5:19–28.

Wallin H., P.A. Chiverton, B.S. Ekmob & A. Borg. 1992. Diet, fecundity and egg size in some polyphagous predatory carabid beetles. Entomologia Experimentalis et Applicata 65:129–140.

Wasserman, S.S. & T. Asami. 1985. The effect of maternal age upon fitness of progeny in the southern cowpea weevil, *Callosobruchus maculatus*. Oikos 45:191–196.

Weygoldt, P. 2000. Whip Spiders (Chelicerata: Amblypygi): Their Biology, Morphology and Systematics. Apollo Books, Stenstrup.