3. Chen, W. P. and Molnar, P., Source parameters of earthquakes and intraplate deformation beneath the Shillong plateau and northern Indo-Burman ranges. *J. Geophys. Res.*, 1990, **95**, 12,527–12,552.

4. Kumar, D., Reddy, D. V. and Pandey, A. K., Paleoseismic investigations in the Kopili fault zone of North East India: Evidences from liquefaction chronology. *Tectonophysics*, 2016, **674**, 65–75.

5. Person, W. J. (ed.), Seismological notes – January–February, *B. Seismol. Soc. Am.*, 1988, **78**, 2115–2119.

6. US Geological Survey, *M* 6.7–30 km W of Imphal, India, 24 January 2016; http://earthquake.usgs.gov/earthquakes/eventpage/us10004b2n#executive

7. Indian standard criteria for earthquake resistant design of structures: Part 1 – General provisions and buildings, Bureau of Indian Standards, New Delhi, 2002, IS: 1893 (Part 1).

8. Wald, D. J., Quitoriano, V., Heaton, T. H. and Kanamori, H, Relationships between peak ground acceleration, peak ground velocity, and modified Mercalli intensity in California. *Earthq. Spectra*, 1999, **15**, 557–564.

9. Linkimer, L., Relationship between peak ground acceleration and modified Mercalli intensity in Costa Rica. *Rev. Geol. Am. Central*, 2008, **38**, 81–94.

10. Indian standard ductile detailing of reinforced concrete structures subjected to seismic forces – Code of practice, Bureau of Indian Standards, New Delhi, 1993, IS: 13920.

11. Indian standard seismic evaluation and strengthening of existing reinforced concrete buildings – Guidelines, Bureau of Indian Standards, New Delhi, 2013, IS: 15988.

12. Indian standard seismic evaluation, repair and strengthening of masonry buildings – Guidelines, Bureau of Indian Standards, New Delhi, 2009, IS: 13935.

13. Indian standard plain and reinforced concrete – Code of practice, Bureau of Indian Standards, New Delhi, 2002, IS: 456.

14. Kaushik, H. B. and Dasgupta, K., Assessment of seismic vulnerability of structures in Sikkim, India, based on damage observation during two recent earthquakes. *J. Perform. Constr. Facil.*, 2013, **27**, 697–720.

15. Rai, D. C., Mondal, G., Singhal, V., Parool, N., Pradhan, T. and Mitra, K., Reconnaissance report of the *M* 6.9 Sikkim (India–Nepal border) earthquake of 18 September 2011. *Geomat. Nat. Haz. Risk*, 2012, **3**, 99–111.

Negative allometry for egg size in ladybeetles (Coleoptera: Coccinellidae): Trade-off between egg hatch time and size

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Similar to a wide range of other organisms, large species of predatory ladybeetles lay proportionally small eggs when compared to smaller species. This study determines whether egg size in aphidophagous lady beetles is constrained by the time it takes for the eggs to hatch. The eggs of the large species, *Anisolemnia dilatata* (168 mg), and small species of ladybeetle, *Coccinella septempunctata* (27 mg), were collected immediately after they were laid, separated from one another and weighed. The time for the egg to hatch was determined at 22°C. As predicted, the eggs of the large species were a smaller proportion (0.0048) of their mother's weight when compared to the eggs of the small species (0.0061). On an average, the eggs of the large species were about 4.9 times heavier and took 1.31 times longer to hatch than those of small species. These results indicate that in insects and aphidophagous ladybeetles, in particular, egg hatch time is not directly proportional to the egg size and reproduction may involve more than a trade-off between the number of eggs and size. It is likely that egg hatch time is a constraining factor and an important determinant of the inter-specific negative allometry for egg size in this group of insects.

Keywords: Egg size, inter-specific negative allometry, ladybeetles.

NEGATIVE allometry for egg size represents a relationship in which the eggs of species with the biggest adults tend to be larger than those produced by smaller adults, but the eggs become proportionally smaller as the adult size increases[1]. Such a relationship is recorded in many groups of animals (spiders[2], insects[3,4], fish[5], turtles[6], snakes[7], lacertid lizards[8], birds[9]). This has mainly been discussed in terms of a trade-off between egg number and size[9,10] according to which bigger adults, within or between species, tend to produce more eggs directly proportional to their body mass and length of reproductive life but invest less in egg size because of ecological and physiological constraints[11,12].

Here, predatory ladybeetles (Coleoptera: Coccinellidae) were used to explain the interspecific allometric relationship between egg size and adult size. Available

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studies on ladybeetles show that there is an ecological constraint on the lower limit of hatchling size as they have to pursue and subdue their aphid prey[3]. Investment in gonads scales with body weight with exponent of 1 and number of eggs per clutch is determined by the number of ovarioles[13]. The developmental time of eggs is also a constraining factor. There is both empirical evidence[14,15] and physiologically based theoretical prediction[16] from ladybeetles which indicate that the duration of incubation at a given temperature increases with egg size. Therefore, any benefits associated with an increase in egg size is counterbalanced by the costs resulting from longer incubation period. In ladybeetles, egg cannibalism is an important mortality factor[17]. Therefore, the increased risk of cannibalism associated with longer incubation times may place an upper limit on egg size in ladybirds.

The specific objectives of this study, therefore, were to test whether (1) negative allometry occurs between adult sizes and egg sizes of the giant species of the predatory ladybeetle, *Anisolemnia dilatata* (F.) and the smaller species, *Coccinella septempunctata* L., (2) that the weights of male and female eggs are similar, and (3) to determine whether the larger eggs of the giant species take significantly longer to hatch than the smaller eggs of the small species.

Laboratory rearing of *A. dilatata* and *C. septempunctata* collected from their natural habitats in Ischanchandnagar (West Tripura district, India) (23°45.669′N and 91°15.967′E, Ele: 34 m) was done. Males and females in pairs were kept in 9 cm diameter petri dishes, one pair in each, at 22°C in an environmental chamber and provided *ad libitum* supply of live aphids, *Ceratovacuna silvestrii* (Takahashi) from *Bambusa balcooa* Roxb. for *A. dilatata*, and *Aphis craccivora* Koch from *Lablab puroueus* (L.) for *C. septempunctata* following Agarwala and Majumder[17]. All the females of the two species laid eggs in clusters. The eggs were moistened with water and then separated using a fine paint brush. Fifteen such eggs were collected from each of the 10 pairs of the two species, surface-dried by placing on dry filter paper, weighed on a micro-balance to an accuracy of 2 μg, placed individually in a 5 cm petri dish at 22°C, and observed every hour until they hatched. Individuals of these neonates, 100 each of *A. dilatata* and *C. septempunctata*, were reared separately until they reached the adult stage and their sex was determined. Hatch time, which is the time in hours from laying to hatching, was recorded for individual eggs. Hatchlings of the two species were fed first instar aphids of their respective aphid preys, and reared to the adult stage on *ad libitum* supply of mixed instars of live aphids in order to determine their sex. Larvae from all the eggs that hatched completed their development and emerged as adults. Weights and hatch time of forty eggs that hatched and produced males and females were recorded for the two species studied. It was expected that the weights of the male and female eggs of each species

would be similar[18]. Egg size by fresh weight and egg hatch time of large and small species of ladybeetles were subjected to two-way ANOVA for interaction between sex and species.

Average weights of eggs and hatch times of both sexes of the two species are given in Tables 1 and 2. A two-way ANOVA of the weights of eggs expressed as a proportion of the mother's weight indicates a significant interaction (sex) × (species) ($F = 2.86$, $df = 3,157$, $P < 0.001$). Both the species invested similar proportions of their body weight in male and female eggs (*A. dilatata*: $F = 16.76$, $df = 1,157$, *NS*; *C. septempunctata*: $F = 13.60$, $df = 1,157$, *NS*). Based on the pooled results, *A. dilatata* invested proportionally less in each egg (0.0048) than *C. septempunctata* (0.0061) (one way ANOVA: $F = 3.59$, $df = 1,159$, $P < 0.001$). Similarly, a two-way ANOVA of the egg weights indicates a significant interaction between sex and species ($F = 3.44$, $df = 3,157$, $P < 0.05$). The average weights of the male and female eggs of the two ladybird species did not differ significantly (*A. dilatata*: $F = 15.47$, $df = 1,157$; *NS*; *C. septempunctata*: $F = 15.47$, $df = 1,157$, *NS*) (Table 1). However, the pooled weight of the eggs of *A. dilatata* (0.819 mg) differed significantly from that of the eggs of *C. septempunctata* (0.167 mg; one way ANOVA: $F = 1.74$, $df = 1,158$, $P < 0.001$; Table 2).

A two-way ANOVA of hatch times indicated significant interaction between species and sex ($F = 2.73$, $df = 3,157$, $P < 0.05$). The average hatch times of the male and female eggs of each species did not differ significantly (hatch times, *A. dilatata*: $F = 2.76$, $df = 1, 79$, *NS*; *C. septempunctata*: $F = 13.01$, $df = 1, 79$, *NS*), as determined in the ladybeetle, *Adalia bipunctata* (L.)[19]. However, the pooled hatch times of *A. dilatata* differed significantly from that of *C. septempunctata* ($F = 1.49$, $df = 1,158$, $P < 0.001$).

Although the larger species, *A. dilatata*, lays much larger eggs than the smaller *C. septempunctata*, in terms of investment per egg, large species eggs are a smaller proportion of their mother's weight (0.0048) than eggs of the smaller species (0.0061). This result is in accordance with the prediction of an inter-specific allometric study of egg size relative to adult size in aphidophagous ladybeetles[20]. That is, as in other groups, large species produce proportionally smaller eggs than small species. Combining the results for *A. dilatata* with the data in Stewart *et al.*[19] and re-analysing the combined results did not affect the exponent relative to body mass in the relationship between egg weight and adult weight, which remained the same (0.63). If *A. dilatata* invested the same amount of mass per egg per unit body mass as *C. septempunctata* then its eggs would weigh 1.08 mg, which is 35% more than that recorded in this study.

Results show that larger eggs of *A. dilatata* take significantly longer time to hatch than smaller eggs of *C. septempunctata*. This agrees with empirical data for other

Table 1. The weights of female adults of *Anisolemnia dilatata* and *Coccinella septempunctata*, their eggs and the time it takes the eggs to hatch at 22°C

Species	Female adult weight (mg)	Male eggs			Female eggs		
		Wt (mg)	Proportion of mother's wt	Hatch time (h)	Wt (mg)	Proportion of mother's wt	Hatch time (h)
A. dilatata	168.36 ± 1.24^a ($n = 40$)	0.769 ± 0.003^a ($n = 40$)	0.0045 ± 0.00002^a ($n = 40$)	110.06 ± 0.36^a ($n = 40$)	0.881 ± 0.002^a ($n = 40$)	0.0052 ± 0.0001^a ($n = 40$)	111.42 ± 0.68^a ($n = 40$)
C. septempunctata	27.14 ± 0.32^b ($n = 40$)	0.168 ± 0.001^b ($n = 40$)	0.0062 ± 0.00003^b ($n = 40$)	83.62 ± 0.51^b ($n = 40$)	0.171 ± 0.002^b ($n = 40$)	0.0063 ± 0.0001^b ($n = 40$)	84.12 ± 0.78^b ($n = 40$)

Dissimilar alphabets in superscripts accompanying mean $\pm$ SEM values in a column denote significant differences by Student's *t*-test (unpaired: $P < 0.05$).

Table 2. The pooled weights of male and female adults of *A. dilatata* and *C. septempunctata*, their eggs and the time it takes the eggs to hatch at 22°C

Species	Pooled of males and females		
	Wt (mg)	Proportion of mother's weight	Hatch time (hr)
A. dilatata	0.819 ± 0.046^a ($n = 80$)	0.0048 ± 0.0001^a ($n = 80$)	109.89 ± 0.73^a ($n = 80$)
C. septempunctata	0.167 ± 0.035^b ($n = 80$)	0.0061 ± 0.00004^b ($n = 80$)	83.87 ± 0.83^a ($n = 80$)

Footnote same as in Table 1.

groups of animals[9,14] and indicates that there is a possibility of cause–effect relationship between egg size and hatch time. However, more data on egg hatch times and the numbers of eggs laid for a wide range of species of different sizes is needed to define the form of this relationship.

Is a long hatch time necessarily disadvantageous? As in other insects, mortality during the egg stage in ladybeetle is high. Field and laboratory studies indicate that egg mortality is mainly due to cannibalism[20] and is strongly density-dependent[21,22]. However, intra-guild predation is possibly less important because the eggs are often well-defended chemically against insect predators[23,24]. Thus there is evidence to indicate that mortality during early development could be important in determining investment in individual offspring. This should be reflected in the number of eggs laid per female of the two species. Differences in life-time fecundity should be considered in future discussions on the evolutionary and ecological significance of egg size variation.

1. Garcia-Barros, E., Taxonomic patterns in the egg to body size allometry of butterflies and skippers (Papilionidae & Hesperiidae). *Nota Lipid*, 2004, **25**, 161–175.
2. Marshall, S. D. and Gittleman, J. L., Clutch size in spiders: is more better? *Func. Ecol.*, 1994, **8**, 118–124.
3. Stewart, L. A., Dixon, A. F. G., Růžicka, Z. and Iperti, G., Clutch and egg size in ladybird beetles. *Entomophaga*, 1991, **36**, 93–97.
4. García-Barros, E., Body size, egg size, and their interspecific relationships with ecological life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biol. J. Linn. Soc.*, 2000, **70**, 251–284.
5. Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R. and Sams, S., Relationships between body size and some life history parameters. *Oecologia*, 1978, **37**, 257–272.
6. Elgar, M. A. and Heaphy, L. J., Covariation between clutch size, egg weight and egg shape: comparative evidence for chelonians. *J. Zool.*, 1989, **219**, 137–152.
7. Shine, R., Harlow, P. S., Keogh, J. S. and Boeadi, K., The allometry of life-history traits: insights from a study of giant snakes (*Python reticulatus*). *J. Zool.*, 1998, **244**, 405–414.
8. Bauwens, D. and Díaz-Uriarte, R., Covariation of life-history traits in lacertid lizards: a comparative study. *Am. Nat.*, 1997, **149**, l91–111.
9. Rahn, H., Paganelli, C. V. and Ar, A., Relation of avian egg weight to body weight. *The Auk*, 1975, **92**, 750–765.
10. Anderson, J., The size of spider eggs and estimates of their energy content. *J. Arach.*, 1990, **18**, 73–78.
11. Berrigan, D., The allometry of egg size and number in insects. *Oikos*, 1991, **60**, 313–321.
12. Lloyd, D. G. Selection of offspring size at independence and other size-versus number strategies. *Am. Nat.*, 1987, **129**, 800–817.
13. Dixon, A. F. G., Body size and resource partitioning in ladybirds. *Pop. Ecol.*, 2007, **49**, 45–50.
14. Sinervo, B., The evolution of maternal investment in lizards: an experimental and comparative analysis of egg size and its effect on offspring performance. *Evolution*, 1990, **44**, 270–294.
15. Birchard, G. F., Walsh, T., Roscoe, R. and Reiber, C. L., Oxygen uptake by komodo dragon (*Varanus komodensis*) embryos: the energetics of prolonged development. *Physiol. Zool.*, 1995, **65**, 622–633.
16. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B., Towards a metabolic theory of ecology. *Ecology*, 2004, **85**, 1771–1789.
17. Dixon, A. F. G., *Insect Predator-Prey Dynamics: Ladybird Beetles and Biological Control*, Cambridge University Press, Cambridge, 2000.
18. Agarwala, B. K. and Majumder, J., Life history fitness of giant ladybird predator (Coleoptera: Coccinellidae) of wooly aphids

(Hemiptera: Aphididae) in varying prey densities from northeast India. *Curr. Sci.*, 2016, **110**, 434–438.

19. Yasuda, H. and Dixon, A. F. G., Sexual size dimorphism in the two spot ladybird beetle *Adalia bipunctata*: developmental mechanism and its consequences for mating. *Ecol. Entomol.*, 2002, **27**, 493–498.

20. Stewart, L. A., Hemptinne, J.-L. and Dixon, A. F. G., Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. *Func. Ecol.*, 1991, **5**, 380–385.

21. Osawa, N., Sibling and non-sibling cannibalism by larvae of a ladybeetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in the field. *Res. Pop. Ecol.*, 1989, **31**, 153–160.

22. Agarwala, B. K. and Dixon, A. F. G., Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecol. Entomol.*, 1992, **17**, 303–309.

23. Agarwala, B. K. and Dixon, A. F. G., Why do ladybirds lay eggs in clusters? *Func. Ecol.*, 1993, **7**, 541–548.

24. Agarwala, B. K. and Bhowmik, P. J., Effect of chemical defence on the fitness of ladybird predator, *Cheilomenes sexmaculata* (Fabricius). *J. Biol. Control*, 2007, **21**, 89–96.

Application of indigenously developed remotely operated vehicle for the study of driving parameters of coral reef habitat of South Andaman Islands, India

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Coral reef biodiversity in South Andaman Islands, India was studied using indigenously developed remotely operated underwater vehicle, PROVe. The vehicle was manoeuvred in coral reef habitats using underwater navigational aids to record faunal assemblages along with underwater spatio-temporal spectral irradiance characteristics coupled with surface radiance, water temperature, salinity and underwater visuals by high-definition camera devices. PROVe-based observations and the outcome from scientific payloads indicated that it will be a new additional tool for the Indian scientific community to map coral reef habitats, correlate and validate the satellite-derived parameters to understand coral reef health.

Keywords: Coral reef, driving parameters, remotely operated vehicle, spectral irradiance.

MARINE biodiversity of the Andaman and Nicobar (A&N) Islands, India is remarkable with its rich assemblages of coral reef distribution within 6°–14°N lat. and 92°–94°E long. (ref. 1). Islands of the Andaman have an estimated coral reef area of 934.26 sq. km and can be grouped into North Andaman, Middle Andaman and South Andaman regions[2]. Among these island groups, South Andaman is rich in biodiversity; all the reefs have small reef flat and gradual reef slope with good luminosity, and good coral live cover along with dead corals and rubbles[3].

Coral reef occurrences are governed by the symbiotic relationship of coral community with dinoflagellates (zooxanthelle). Sunlight irradiance intensity and spectral characteristics change with depth and play a critical role in the structuring of shallow-water coral reef community[4–6]. Solar irradiation (heat budget) and nutrients play a supportive role in the survival of algal cells which may break down due to thermal stress and lead to bleached appearance of corals at higher temperature[7,8]. Study of shallow-water coral habitats suggests that the production of suitable proteins as host strategy is important to protect the symbiotic algae from high irradiance by absorbing photons or by reemission[9,10]. Important environmental factors affecting the ecology of reef-forming, symbiont-bearing corals are the quantity and quality of light[11]. It is an established fact that zooxanthellae algae generate oxygen photosynthesis which supports 95% of respiratory demand of the coral community[12]. Hence the measure of light for such photosynthesis in terms of availability of photons is the critical parameter to understand the ecology of the shallow-water coral community. It is a measure of radiant power and is defined in terms of photon (quantum) flux, specifically the number of moles of photons in the radiant energy between 400 and 700 nm.

Several methodologies have been followed worldwide to map the coral reef habitats. Survey techniques include underwater observations by scuba and snorkel divers, visual quadrant methods[13], manta tow, random swims/timed swims, point intercept transects or line intercept transects with triangulation references[14,15], high-resolution mapping from airborne lidar[16], multispectral remote sensing imagery, underwater towed digital

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