

Predator size and prey size: presumed relationship in the mantid *Hierodula coarctata* Saussure

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Measurements of tibia length and tibial hook angle were used to calculate optimum prey size in 714 specimens of the mantid *Hierodula coarctata*. These values were then regressed on the cube root of dry body weight to derive a presumed predator-prey size relationship for the species. Energetic arguments are advanced to account for the observed relationship. An interspecific relationship is also demonstrated for three species of mantids and two species of mantis shrimp (stomatopod crustaceans).

Introduction

The ecological literature documents predator-prey size relationships for a variety of predator species. Both intraspecific and interspecific relationships have been shown to exist. The former are ordinarily derived by examining the food sizes taken by various sizes of one species of predator, either in the field or in the laboratory. This has been done for many species, including a variety of fishes (Hartman 1958; Jackson 1960; Shelbourne 1962), anoline lizards (Schoener 1967; Schoener and Gorman 1968; Roughgarden 1974), snails (Fenchel 1975), spiders (Turnbull 1960), and frogs (Turner 1959). Such data are useful in understanding the evolved growth strategies of the species concerned. It is the primary purpose of this paper to demonstrate a presumed predator size - prey size relationship in the mantid *Hierodula coarctata* Saussure.

Interspecific predator-prey size relationships are generally derived by comparing the mean sizes of prey taken by the average adult-sized individual of various species. This has been done, for example, for several groups of birds (Gibb 1956; Schoener 1968; Hespeneheide 1971), predatory wasps and flies (Hespeneheide 1973), and carnivorous mammals (Rosenzweig 1966). Where the species concerned are sympatric, the data are useful in the testing of species-packing models and theories of community evolution. By using the same technique as that employed for the mantid data, we have constructed an interspecific prey-predator size relationship for six

species of raptorial arthropods (mantids and mantis shrimps). This relationship will be briefly noted in the discussion.

Methods and Materials

One of us (Holling 1964) has shown that the preferred prey size of the mantid *Hierodula crassa* is the maximum size of prey that can be securely held without violating the locking principle of the grasping foreleg. This optimum size (r) may be determined from the equation

$$[1] \quad r = T \sin(\beta - \alpha)/2,$$

where T is the length of the tibia (millimetres), α is the tibial hook angle (degrees), and β is the angle between the femur and the tibia when (a) the prey touches the tip of the tibial hook, the tibia, and the femur and (b) a line drawn from the tip of the tibial hook perpendicular to the femur runs through the centre of the prey.

Once α is known, β can be calculated iteratively from the equation

$$[2] \quad \tan(\beta - \alpha) = 2 \tan(\beta/2).$$

We measured α and T for 714 individual *H. coarctata* (instars 1 to 8 and adults of both sexes) and calculated optimum prey size from equations 1 and 2, assuming that the relationship holds for this species of *Hierodula*. Figure 1 shows how the measurements were taken. Dry body weights were determined for the same individuals by drying to constant weight at 37 °C. Regressions of optimum prey size against dry weight and (dry weight)³ were then calculated.

Results

The plot of optimum prey size against body weight has a pronounced curvature. However, that of optimum prey size against (body weight)³ is virtually linear (Fig. 2). This transformation

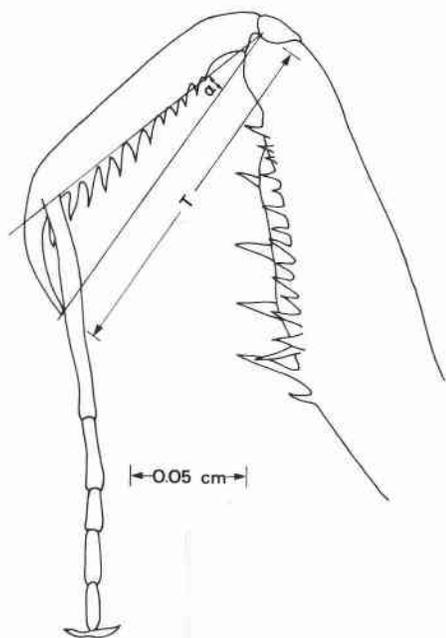


FIG. 1. The grasping foreleg of *H. coarctata*, showing tibia length (T) and tibial hook angle (α).

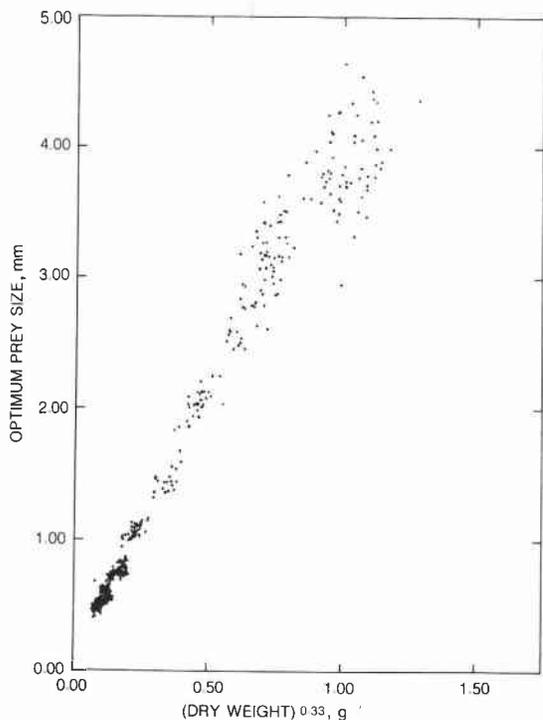


FIG. 2. The relationship between optimum prey size (millimetres), predicted from equations 1 and 2, and the cube root of dry body weight (grams) for *H. coarctata*.

was chosen because in theory the length of any portion of an animal's body should be related to the cube root of its body weight. In effect Fig. 2 is a plot of prey diameter against predator length. The equation best describing the data is

$$[3] \text{ optimum prey size} = 0.174 + 3.808(\text{dry weight})^{0.33}$$

and is significant at $p < 0.005$.

Regressions of tibial hook angle (α) and of tibia length (T) on dry weight were also carried out. The equations

$$[4] \quad \alpha = 11.181 + 1.544(\text{dry weight})^{0.33}$$

and

$$[5] \quad T = 0.488 + 9.741(\text{dry weight})^{0.33}$$

were also significant at $p < 0.005$. A regression of β on dry weight would be meaningless as β was not measured independently.

Equation 5 simply shows that the tibia grows allometrically with the rest of the body. In itself this would result in a linear increase in prey size as the mantid grows (see equation 1). However, tibial hook angle also increases, causing a slightly more rapid rate of change of optimum prey size than would otherwise be the case. The effects of tibia length and hook angle can be separately assessed. If tibial hook angle were constant (at 11.181°), β (from equation 2) would be 60.667° . Substituting these values and equation 5 into equation 1 gives

$$[6] \text{ optimum prey size} = 0.186 + 3.703(\text{dry weight})^{0.33}$$

For a 5.0-g mantid, this would reduce optimum prey size from 6.69 to 6.52 cm. Obviously, tibia length is the major contributor to the increase in prey size with increased mantid size.

Discussion

The major assumption underlying the methodology is that the preferred prey size for any sized individual of *Hierodula coarctata* may be predicted from equation 1, as is true for adult female *H. crassa* (Holling 1964). Experimental verification of this is ultimately required, but in the meantime the relationship will be assumed to hold. If the approach is warranted, its significance is that the preferred prey size of mantids may be inferred from morphological studies of

museum specimens rather than by gut analysis. The situation may sometimes be more complex. According to Hespenheide (1973), for example, different prey taxa have different mean sizes in the diet of a single species of swift. However, the gut analysis method has its own inherent problems as it is usually not possible to determine whether the animal prefers food of a particular size or is forced to eat it because of competition with other species, i.e. it is difficult in practice to distinguish the fundamental from the realized niche (Hutchinson 1957).

Functional morphology arguments have previously been used to predict food size for filter-feeding fish (e.g. Magnuson and Heitz 1971), birds (e.g. Willson 1972; Lederer 1975), and aquatic invertebrates (e.g. Maly and Maly 1974). To our knowledge the approach has not previously been used to determine predator-prey size relationships in terrestrial invertebrates.

As an animal grows, its basal and standard metabolic rates (MR) increase according to the formula

$$[7] \quad MR = a(\text{body weight})^b,$$

where a and b are empirically derived constants. The b 's vary from 0.5 to 1.0 but cluster about 0.75 (Schoener 1969). As a result large predators require more or larger prey than do small ones. If the predator's strategy is to take the same number of increasingly larger prey as it grows, then optimum prey size should increase with predator size, as it does for *Hierodula coarctata* and almost all other species of predator studied to date (references in the Introduction). The iguanid lizard *Sceloporus magister* is one apparent exception to this rule (Parker and Pianka 1973).

However, if the observed relationship for the mantid were related solely to metabolic rate and the number of captures remained constant, then the weight of the prey (optimum prey size)³ would be linearly related to (body weight)^{0.75} and the curve of optimum prey size against (body weight)^{0.33} would have a pronounced negative acceleration not evident in the data. This may mean that the mantid captures fewer prey as it grows but that these prey are correspondingly larger. Numerical prey density probably decreases with increasing prey size, and this would have the effect of increasing searching time and energy expenditure per captured prey. Furthermore large prey require a longer handling

time and consequent higher energy expenditure than do small ones (e.g. Werner 1974). All of these factors could cause optimum prey size to increase faster with predator size than would be predicted from the metabolic rate - body weight function alone. In addition such behavioural parameters as reactive distance and attack velocity quite likely vary with predator size. It is therefore impossible to be certain whether the optimum prey size for a particular predator size is energetically optimal, although we would expect this to be the case.

The methodology used ignores other parameters of the predator-prey size function. It is quite likely that niche breadth increases with predator size as a result of increasing variance and (or) skew of the size distribution of prey eaten. This has been documented for many species (e.g. finches, Pulliam and Enders (1971); sunfish, Hall *et al.* (1970); plaice larvae, Shelbourne (1962)) and may or may not be true for mantids.

The method used to predict optimum prey size was also applied to four other species of raptorial arthropods: the mantids *Tenodera australasia* ($n = 14$) and *Mantis religiosa* ($n = 42$), and the stomatopods (mantis shrimp) *Pseudosquilla ciliata* ($n = 17$) and *Oratosquilla oratoria* ($n = 3$). Measurements were obtained in a manner identical with that for *H. coarctata*, except that the length and hook angle of the dactyl (distal segment of the second maxilliped) were measured on the stomatopods. The interspecific predator-prey size relationship is shown in Fig. 3. Here, again, optimum prey size increases in a linear way with increasing predator size. However, great care is required in interpreting these data. Firstly, it is not known whether the underlying assumption is valid across species within one genus, let alone across classes within a phylum. Secondly, it is not at all certain that stomatopods use their raptorial appendages in a manner analogous to the mantids', despite the great morphological similarities between them. According to Caldwell and Dingle (1975), it is most common for these stomatopods to spear soft-bodied prey with the sharp dactyl spines. It is for these reasons that the interspecific data are noted parenthetically at this point rather than in the results section.

Despite these reservations, however, the 'goodness' of the relationship between optimum prey size and cube root of body weight argues against its being solely coincidental. We suggest that a

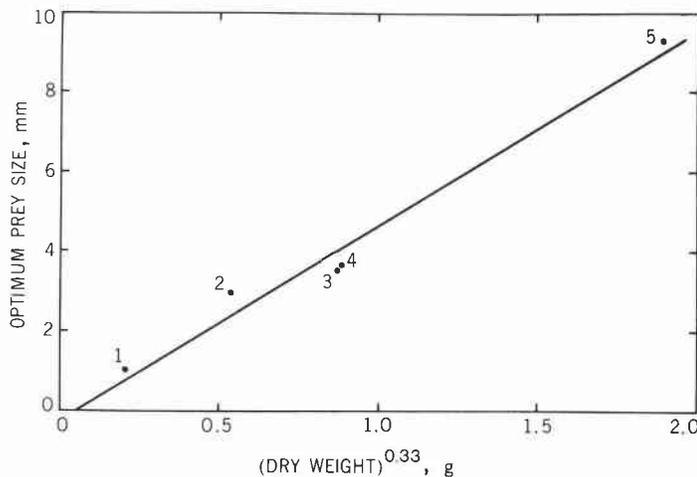


FIG. 3. The relationship between mean optimum prey size (millimetres), predicted from equations 1 and 2, and the cube root of mean dry body weight (grams) for five species of raptorial arthropods. Key: 1, *Mantis religiosa*; 2, *Tenodera australasia*; 3, *H. coarctata* (adults, $n = 93$); 4, *Pseudosquilla ciliata*; 5, *Oratosquilla oratoria*. For other sample sizes, see text.

single relationship exists for this diverse group of predatory arthropods and that, at the minimum, the relationship has descriptive utility. The equation best describing the data is

$$[8] \text{ optimum prey size} = -0.136 + 4.806(\text{dry weight})^{0.33}$$

and is significant at $p < 0.01$.

When regressions of prey size on predator size are separately conducted for each species and the regression coefficients compared, the slopes are significantly different ($p < 0.05$) in 5 out of 10 comparisons, and the intercepts, in all 10. When similar comparisons (78) are made for the various instars and sexes of the *H. coarctata* data (13 groups), the slopes are significantly different 16 times and the intercepts 56 times. In both cases, however, these differences are insignificant in the context of the overall relationships, where the small individual line segments are not scattered randomly across the graph but are arrayed along a line of their own. The situation is highly reminiscent of that seen when territory or home range size is plotted against log body weight (McNab 1963; Schoener 1968). In these cases birds or mammals with different foraging strategies have different regression coefficients, but a rather precise overall relationship still exists. Both the territory and food size data demonstrate the pervasive influence of energetics on the ecological processes of animals.

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- CALDWELL, R. L., and H. DINGLE. 1975. Ecology and evolution of agonistic behavior in stomatopods. *Naturwissenschaften*, **62**: 214-222.
- FENCHEL, T. 1975. Character displacement and coexistence in mud snails (Hydrobiidae). *Oecologia* (Berlin), **20**: 19-32.
- GIBB, J. 1956. Food, feeding habits, and territoriality in the rock pipit (*Anthus spinoletta*). *Ibis*, **98**: 506-530.
- HALL, D. J., W. E. COOPER, and E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* **15**: 839-928.
- HARTMAN, G. F. 1958. Mouth size and food size in young rainbow trout, *Salmo gairdneri*. *Copeia*, **1958**: 233-234.
- HESPENHEIDE, H. A. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to Tyrannidae. *Ibis*, **113**: 59-72.
- . 1973. Ecological inferences from morphological data. *Annu. Rev. Ecol. Syst.* **4**: 213-229.
- HOLLING, C. S. 1964. The analysis of complex population processes. *Can. Entomol.* **96**: 335-347.
- HUTCHINSON, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* **22**: 415-427.
- JACKSON, P. B. N. 1960. The impact of predation on African freshwater fishes. *Proc. Zool. Soc. London*, **136**: 603-622.

- LEDERER, R. J. 1975. Bill size, food size, and jaw forces of insectivorous birds. *Auk*, **92**: 385-387.
- MAGNUSON, J. J., and J. G. HEITZ. 1971. Gill raker apparatus and food selectivity among mackerels, tunas and dolphins. U.S. Nat. Ocean Atmos. Admin., Fish. Bull. **69**: 361-370.
- MALY, E. J., and M. P. MALY. 1974. Dietary differences between two cooccurring calanoid copepod species. *Oecologia* (Berlin), **17**: 325-333.
- MCNAB, B. K. 1963. Bioenergetics and the determination of home range size. *Am. Nat.* **97**: 133-140.
- PARKER, W. S., and E. R. PIANKA. 1973. Notes on the ecology of the iguanid lizard, *Sceloporus magister*. *Herpetologica*, **29**: 143-152.
- PULLIAM, H. R., and F. ENDERS. 1971. The feeding ecology of five sympatric finch species. *Ecology*, **52**: 557-566.
- ROSENZWEIG, M. L. 1966. Community structure in sympatric carnivora. *J. Mammal.* **47**: 602-612.
- ROUGHGARDEN, J. 1974. Niche width: biogeographic patterns among *Anolis* lizard populations. *Am. Nat.* **108**: 429-442.
- SCHOENER, T. W. 1967. The ecological significance of sexual dimorphism in size of the lizard *Anolis conspersus*. *Science*, **155**: 474-477.
- 1968. Sizes of feeding territories among birds. *Ecology*, **49**: 123-141.
- 1969. Models of optimal size for solitary predators. *Am. Nat.* **103**: 277-313.
- SCHOENER, T. W., and G. C. GORMAN. 1968. Some niche differences among three species of Lesser Antillean anoles. *Ecology*, **49**: 819-830.
- SHELBOURNE, J. E. 1962. A predator prey size relationship for plaice larvae feeding on *Oikopleura*. *J. Mar. Biol. Assoc. U.K.* **42**: 243-252.
- TURNBULL, A. L. 1960. The prey of the spider *Linyphia triangularis* (Clerck) (Araneae, Linyphiidae). *Can. J. Zool.* **38**: 859-873.
- TURNER, F. B. 1959. An analysis of the feeding habits of *Rana p. pretiosa* in Yellowstone Park, Wyoming. *Am. Midl. Nat.* **61**: 403-413.
- WERNER, E. E. 1974. The fish size, prey size, handling time relationship in several sunfishes and some implications. *J. Fish. Res. Board Can.* **31**: 1531-1536.
- WILLSON, M. F. 1972. Seed size preference in finches. *Wilson Bull.* **84**: 449-455.