

## MODELS OF OPTIMAL SIZE FOR SOLITARY PREDATORS

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Prediction of an optimal predator size determined primarily by trophic-energetic relationships arises from the interaction of two sets of factors: the abundances of different food items and the relative amounts of energy extractable from these items by predators of a given size. Where very similar competing species are absent, as for "solitary" species, that is, those monopolizing a more or less discrete energy source, major discontinuities and irregularities in functions describing food abundance should be relatively infrequent, making prediction of optimal size more consistent. In addition to providing a logical starting point for a general theory of optimal size, solitary species are in themselves an important component of many faunas, particularly so for depauperate islands but also for mainlands, where the numerous specialist species are able individually to dominate certain kinds of resources.

There are many observations of solitary species that may require quantitative formulation for even partial understanding. For example, in solitary *Anolis* lizard species, there is convergence to a single adult male size from numerous stocks (Schoener, 1967; Schoener, in press). Exceptions tend to cluster around two sizes: a slightly smaller size for northerly species and a much larger size for more equatorial forms. Furthermore, adult females of these species converge to another size, well below that of adult males. In many birds, on the other hand, solitary species show little sexual dimorphism (with some outstanding exceptions: Selander, 1966). A desirable model would specify the conditions favoring several sizes and factors significantly affecting distances between them. To consider a second example, it has been observed for several archipelagos that lizards of a given taxon are often larger when solitary than when in the presence of similar species (Soulé, 1966; Schoener, in press). Again, knowing the optimal size or modal sizes for a solitary species and by what means these might be changed furnishes hypotheses as to the impact of potential competitors.

In this paper I present models predicting optimal size for several types of predators, largely definable on the basis of how they locate and overtake their prey and how they allocate their feeding time throughout their entire activity period. For the sake of simplicity and maximum contrast, two extreme types of predators are first considered, neither of which is completely realistic. One expends time and energy in pursuit, handling, and

swallowing of items but not in search, whereas the other expends time and energy in search, handling, and swallowing but not in pursuit. All models have three major restrictions. First, the energy yields and abundances of food items are calculated with respect to size of these items only. Second, for a class of predators identical except in size, that sized predator is considered optimal which is able to obtain enough food to support its requirements in the least amount of feeding time. Finally, of course, the predator is assumed to be at an optimal size as predicted from trophic relationships alone. Whether it is is partially dependent on the steepness of the optimality gradient, a property which the models also specify. The models should be most valuable in predicting fitness for animals whose number of offspring produced is not physiologically dependent upon body size (e.g., larger body size implying larger ovaries and hence more eggs) and whose number of reared offspring is best increased by augmenting the time available to parents for reproductive and anti-predator activities (see Gadgil and Bossert, in preparation, for a more general approach to this problem).

#### TYPE I PREDATORS

##### *The General Model*

A Type I predator is assumed to passively locate its prey by scrutinizing an area surrounding its vantage point and to be programmed for going after an item or not on the basis of that item's size and distance. While watching for items to enter its possible field of prey capture, the predator is concurrently carrying on other important activities such as maintaining a territory, grooming, looking out for predators, and monitoring potential mates. Although in reality the energy expended in the latter does to some degree affect prey availability, it was desired at first to simulate, using MacArthur and Levins' (1964) terminology, a pure pursuer: that is, one for which the search for food costs nothing above what would have to be expended anyway in other activities.

A computer program was designed which selects that range of food items, indexed in terms of both food length,  $i$ , and distance from the predator,  $r$ , which enables the predator to satisfy its requirements while spending as little time as possible in feeding activities. The procedure of selection is as follows. For a given length of predator,  $B$ , and for each interval of distance from the predator, the net energy per unit time obtained from items after they have been captured and eaten is calculated for all food-size intervals within which this net energy is positive. Additionally, the number of items belonging to a given size and distance interval expected to appear in the potential hunting range of the predator during some large cyclic time period (or fraction thereof) is determined. The energy requirements of the predator over that large period of time are also calculated.

The program then selects that item of food (indexed both by size and distance) which produces the greatest energy gain per unit time. It multiplies the net energy from a single item of that food by the total number of such items to be expected over the large time period. The resulting energy is

compared with the energy requirements of the predator for that period. If it is greater than those requirements, the time taken by the predator to eat just enough items to support itself is printed out; if it is less than those requirements, the next best item is selected and the procedure repeated, the energy obtained over the large time interval from the new items added to that obtained from the previous items, and the time taken to eat these items added to the previous total eating time. Successive comparisons are made either until enough energy is finally obtained to satisfy the predator's requirements, in which case the total feeding time,  $T$ , is printed out, or until all items which produce an energy gain are used up, in which case the predator is not viable in the particular environment being considered. The  $T$ 's are calculated for a range of sizes of predators of a given type and these are compared to determine the optimal predator size.

It is important to realize that the procedure used to select the optimal range of food items, that is, starting from the best and working down, is *not* the order in which the predator eats those items. Rather, the "ideal" predator will always take an item within that range when it appears but will never take an item outside that range. Clustering of prey or perceptual limitations of the predator, among other factors, may in reality cause the predator to do otherwise.

If it is assumed that during a certain fraction of the predator's total activity period it will be unable to begin a feeding sequence because it is otherwise occupied, then an appropriate "safety factor" can be incorporated into the functions which determine the total number of each item available during the large time interval, provided items are missed in the proportion in which they occur. A safety factor can also be added if the predator is assumed to miss a certain fraction of items pursued, so long as the probability of failure to capture is independent of the sizes of predator and prey. While the probability of capture clearly depends on the sizes of predator and prey in some cases, lack of data makes it difficult to construct a function relating these variables.

Because of fluctuations in the food supply, the relative and absolute abundances of prey sizes over successive time periods will not be identical; consequently, hunger functions to monitor these fluctuations, "telling" the predator when it must eat especially low-yield items and when it can confine itself to the very best ones. For example, Holling (1966) has shown empirically that mantids will travel greater distances to capture prey when hungry than when near satiation. We assume in the simulations that such fluctuations are nonexistent, thus erring in the direction of predicting smaller variances in prey-size ranges and prey-capture radii than actually occur.

Examples which most nearly approximate Type I predators can be hypothesized from a wide range of taxa. The particular organisms that I had in mind when designing this program were *Anolis* lizards. These general predators on arthropods spend most of their time perched at a location, favorable for the spotting of prey, from which they are able to carry out various reproductive and social activities as well. Pianka (1966) gives

additional examples of lizards which "sit and wait." Other appropriate organisms might be kingfishers (either those which consume fish or the insectivorous species), many frogs, certain preying mantids, ambush bugs or other kinds of sit-and-wait insect predators, certain predatory cats, many flycatchers, and certain owls.

### *The Rate Curves*

In this section I derive the general expression for calculating net energy per unit time as a function of food particle length and initial distance of the item from the predator. The terms of this equation will be discussed individually. (See Table of Symbols for terms.)

*Pursuit time.*—This term, *TP*, used more specifically than by MacArthur and Pianka (1966), refers only to the time taken by the predator to get close enough to the item to capture it and does not include handling or

TABLE OF SYMBOLS

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$B$	= predator length
$C_4$	= long-term energy requirement level
$C_5$	= prey energy-to-weight proportionality factor
$C_6$	= cost of handling and swallowing
$C_7$	= coefficient of exponential term in <i>THS</i>
$C_8$	= <i>THS</i> if $i \leq i_B$
$C_9$	= cost of pursuing for Type I predator
$C_{10}$	= cost of searching for Type II predator
$C_{11}$	= cost of pursuing for Type IIa predator
$D_1$	= number of prey items available per unit area per large time period (Type I)
$D_2$	= number of prey items available per unit distance (Type II)
$\epsilon_i$	= energy gained per item of available food of size $i$
$F$	= proportion of available food items which Type II predator accepts
$i$	= prey length
$i_B$	= critical prey size for predator size $B$
$K$	= constant for metabolic rate expression
$MR$	= metabolic rate
$n$	= number of available food items Type II predator must encounter to live
$N_1$	= lower bound on food size for Type II predator
$N_2$	= upper bound on food size for Type II predator
$p_i$	= probability (relative abundance) of food class $i$
$r$	= predator-prey distance
$r'$	= prey flight distance
$R_{i,r}$	= fraction of predator energy required per large unit time supplied by prey category $i, r$ per unit time
$T$	= total feeding time per large unit of time
<i>THS</i>	= handling and swallowing time
<i>TP</i>	= pursuit time
<i>TSE</i>	= mean search time per particle of available food
$v$	= prey escape speed
$V$	= predator pursuit speed
$V'$	= predator search speed
$V_B$	= constant in predator size-to-speed expression
$V_I$	= constant in prey size-to-speed expression
$W$	= weight
$\alpha$	= $B/i_B$
$\theta$	= exponent in prey size-to-speed expression
$\lambda$	= exponent in predator energy expenditure expression
$\mu$	= mean of log normal size-abundance distribution
$\sigma$	= standard deviation of log normal size-abundance distribution
$\tau$	= exponent in length-to-weight expression
$\phi$	= exponent in <i>MR</i> expression
$\psi$	= exponent in predator size-to-speed expression

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swallowing time as in their model. Also not included is any time spent by the predator returning to the original perch after prey capture, but this is easily incorporated into  $r$ . For a stationary prey, we assume at first that

$$TP = \frac{r}{V}, \quad (1)$$

where  $V$  is the mean speed of the predator. In this equation  $V$  is not a function of  $B$ . The evidence on this point is incomplete and partially contradictory. Hill (1950) argues that for a group of "similar" animals (as one might expect to find, for example, within the same lower taxon) speed should be independent of size, although larger animals have more staying power. Roughly, this is because the greater linear distance covered in a single movement of a larger animal is counterbalanced by the slower rate at which that movement is taken. Hill shows that for two cetaceans and a variety of medium-to-large terrestrial mammals, speed is in fact independent of size. But Bonner (1965), considering organisms ranging in size from a *Bacillus* to the blue whale (*Balaenoptera*), shows that swimming and running speeds seem to be linearly related to length below a certain large size and that flying speed increases as the cube root of body length (see also Hocking, 1953). But when the organisms he and Hill consider are broken down into taxa, the correlation is poor to nonexistent for several vertebrate groups (birds, lizards, and all but the smallest mammals). It is, however, quite strong for swimming vertebrates smaller than 1 m, and in several fish species (Bainbridge, 1961; Brett, 1965) it even holds between age classes. Since general trends are equivocal for these relations and are likely to be different for different groups, the effect of a  $V$  which is a function of  $B$  on predictions generated by using equation (1) is considered separately below.

If the prey is not stationary, but flees at a speed  $v$ , then  $TP$  becomes more complex. Specifically, if both predator pursuit and prey flight begin at the same instant, if the prey travels  $r'$  distance units before it is caught, and if the predator follows the exact path of the prey, then the predator pursuit and prey flight time are equal and  $(r + r')/V = r'/v$ . Solving for  $r'$ ,

$$r' = \frac{vr}{V - v}. \quad (2)$$

Since a predator may often "head off" its prey,  $r + r'$  is best considered an upper bound on the distance the predator must travel. As above, equation (2) is complicated if  $v$  is a function of  $i$ . For most of the simulations,  $v$  was set equal to zero.

*Handling and swallowing time*—This term,  $THS$ , unlike  $TP$ , should almost always be dependent on  $i$  in relation to  $B$ . Holling (1966) finds that over a very small range of prey sizes it is suitable to consider eating time of mantids as being directly proportional to the weight eaten. However, as Watt (1968) points out, predators which are large relative to their prey and which swallow that prey more or less intact might have a constant eating time. Hence a more general expression might be one in which prey

below a certain critical size,  $i_B$ , are taken in about equal time by a given-sized predator, but above that size are taken in rapidly increasing amounts of time. The  $i_B$ , biologically intuited as the largest prey size readily handled and swallowed by the predator, should of course be a function of  $B$ . Of several possible expressions meeting these qualifications, the following was chosen:

$$\begin{aligned} THS &= C_8, & \text{for } i \leq i_B; \\ THS &= C_8 + C_7 \exp(i - i_B), & \text{for } i > i_B; \end{aligned} \quad (3)$$

$i_B$  is assumed directly proportional to  $B$ :  $i_B = B/\alpha$ . For most simulations  $\alpha$  was set equal to 7. This value is probably reasonable for *Anolis* lizards whose head lengths average about  $\frac{3}{10}$  their snout-vent lengths and whose head widths average about  $\frac{1}{2}$  their head lengths at the gape. The effect of varying  $\alpha$  will be discussed in some detail below. Other multiplicative expressions such as a power function or one in which the exponential growth constant  $\neq 1$  might be equally suitable, but until experimental evidence is gathered on this point, it is best to keep the equations as simple as possible. They do, however, have a major disadvantage which is that  $C_7$  is not a function of  $B$ . While this might be a good approximation for large  $B$ , it is probably poor for very small  $B$ , for it assumes that the increment in time for items a given number of size units beyond  $i_B$  is the same for large and small predators. Biologically, this could be equivalent to assuming that the degree of stretch possible (in linear units) for a trophic aperture is the same regardless of its resting diameter. Suitable modifications might be to complicate  $C_7$  or to place a term inside the exponent.

The biological interpretation of  $C_8$  is the basic time taken to handle and swallow an item. In its broadest interpretation,  $C_8$  might even include the time taken to uncover or hammer through woody or other intervening material to get at an item, provided this were not correlated with  $B$ . The  $C_7$  could be proportional to the degree of rigidity of the predator's trophic apparatus and would be quite low for certain snakes but often high for animals with an inflexible jaw articulation;  $C_7$  represents in part the restriction imposed by the predator's trophic apparatus on taking relatively large-sized prey.

*Energy requirements of the predator.*—The energy requirements of a predator in calories per large time period are assumed given by the expression  $C_4 B^\lambda$ , where  $B$  is predator length and  $C_4$  depends on the duration of the large time period as well as on biological characteristics, such as poikilothermy or homeothermy, of the predator. The  $\lambda$  will depend both on the relation of predator weight to predator length and the relation of predator weight to metabolic rate.

Lengths of animals within particular taxa can often be related to weight in a power function whose exponent  $\tau$  is variable. Using dry weights, I have found that this exponent is usually closer to 2 than to 3 for the arthropod taxa (on an ordinal or adjacent level) examined; cetaceans may show a

similar relationship (Hill, 1950). However, if individuals of taxa belonging to lower categories are considered, the power ought often to be closer to 3, due to the greater uniformity in shape, as is the case, for example, if the *Anolis gundlachi* dimensions measured by Turner, Gist and Rowland (1965) are fitted to a power function. Of course  $\tau$  should often be adaptive, as where there is an advantage in becoming disproportionately long without greatly increasing weight.

Metabolic rate,  $MR$ , can be related to weight,  $W$ , in a power function such as  $MR = KW^\phi$ . In 1960, Hemmingsen combined standard or basal metabolism data from numerous sources to show that the overall  $\phi$  for animals above 0.1–1.0 mg is about 0.73, vertebrate and most invertebrate taxa having  $\phi$ 's clustering about this value. Later determinations for large vertebrate groups tend to fall between 0.6–0.8 (King and Farner, 1961; Lasiewski and Dawson, 1967; Winberg, 1961; Bartholomew and Tucker, 1964). While intraspecific computations can range from 0.5 to over 1, Paloheimo and Dickie (1966) showed that in fish much of this variation is due to differences in temperature and feeding regime. In all simulations,  $\lambda$  was set at 1.5, closer to the low part of the range for vertebrates.

Calculation of  $\lambda$  based on basal or standard metabolic rate assumes that  $\phi$  for those metabolic rates is a satisfactory exponent for actual metabolic rate, which is some average of standard and several active rates in various proportions. Hill (1950) argues theoretically that such should be the case, and Hemmingsen (1960) has demonstrated that  $\phi$ , during "maximal sustained work in homeotherms and apparently insects down to the size of a blowfly," is about 0.73 but seems larger for smaller insects. Once again, smaller taxa show greater variation: Job (1955) showed that  $\phi$  for maximally active metabolism depends on temperature in the trout *Salvelinus fontinalis* being equal to that for standard metabolism at 15° C, but greater or less than that for standard metabolism at temperatures below and above 15° C respectively, though in no case were differences very large. Brett (1965), however, found a greater difference in  $\phi$ 's at 15° C for the salmon *Oncorhynchus nerka* (see below), and Von Bertalanffy (1964) found that  $\phi$  decreases with increasing activity in mice. Paloheimo and Dickie (1966) argue for the relative stability of  $\phi$  as compared to metabolic levels ( $C_4$  in the present model), and their analysis of food consumption in growing fish under different temperature and feeding regimes support that conclusion. Hence, for the sake of generality and analytical simplicity, the constancy of  $\phi$  will be assumed while  $C_4$  will be allowed to vary, though it may well turn out as more measurements are taken that variations in  $\phi$ , however small, will be both predictable and of adaptive significance within certain groups of similar animals.

Holling (1965, 1966) has reviewed his and other studies showing that the number of food items eaten during a certain time period is a monotonically increasing function of prey density up to a certain plateau. However, he points out that at low prey densities the predator could not long survive. The present model assumes that  $C_4B^\lambda$  is near this plateau, and if the maxi-

imum possible energy input is below  $C_4B^\lambda$ , the predator is nonviable. The near constancy of food intake over long periods of time is attested to by Holling's (1959) experiments with mouse predation, in which the predators showed an S-shaped "functional response" to the principal prey though the total food eaten remained constant. Assumption of a constant energy requirement restricts, of course, the domain of the models either to animals using energy input mostly for maintenance or to those requiring energy for reproduction or growth in direct and constant proportion to  $B^\lambda$ . If it is adaptive for organisms to otherwise vary that proportion with respect to body size, a realistic model must become more complex.

*Potential energy of food items*—The energy extractable from a food item of length  $i$  if it costs the predator nothing to pursue, handle, and swallow the item, is assumed directly proportional to the weight of the item and equal to

$$C_5 i^{\tau_i}, \quad (4)$$

where  $\tau_i = 2$  (to the nearest integer) as justified above. Both  $C_5$  and  $\tau_i$  might vary, of course, for food classes with differing proportions of indigestible material or different caloric compositions; these also depend on characteristics of the predator.

*Energy expended in pursuit*—The energy expended between the time the predator begins to move toward the item and the time of capture is assumed equal to

$$C_9 B^{1.5}(TP) \quad \text{or} \quad \frac{C_9 B^{1.5} r}{V}, \quad (5)$$

where  $C_9$  is the cost of pursuing. Note that the exponent of  $B$  for this and the next term is set equal to 1.5, the same value as for the term determining total energy requirements. In the case of a particularly fast predatory mammal, the cheetah, Hill (1950) hypothesizes that to maintain so great an intrinsic muscular speed the output of power must be enormous. This raises the general possibility that when  $V$  is relatively great, either as a function of  $B$  or independent of it,  $C_9$  is correspondingly high. How such an association can partially counterbalance the assumption of speed being independent of size is nicely illustrated by Brett's (1965) data, the only work of its sort I have been able to find. In the salmon *O. nerka* at 15° C,  $\phi$  for maximum activity is greater than  $\phi$  for standard metabolism by 0.19, and length is related to speed during this activity in a power function whose exponent is 0.50. If weight is proportional to the 0.50/0.19 (approximately 2.6) power of length in this species, then the gain in speed with increasing size is exactly canceled out by an increased energy expenditure in expression (5), though not in expression (7).

*Energy expended in handling and swallowing*—This term is assumed equal to

$$C_6 B^{1.5}(THS), \quad (6)$$



where  $C_6$ , the cost of handling and swallowing, is ordinarily much smaller than  $C_9$ . To avoid having to subtract the feeding time from the large time period before determining energy requirements over that large period,  $C_6$  or  $C_9$  should actually be measured as the difference between the absolute cost of a feeding activity and the average cost of nonfeeding activities, algebraically equivalent provided the latter cost is not a function of feeding time and  $\phi$  for different activities does not vary.

No energy deletion is made for that expended in digestion and assimilation, even though it may be a function of  $B$  and  $i$ . There is no easy or obvious way to handle these processes by item, because items are often digested *en masse*. This is particularly true in insectivorous species such as *Anolis* lizards and many birds, found usually with a variety of food sizes in their digestive tracts (see for example Betts, 1955; Schoener, 1967; Schoener and Gorman, 1968; Schoener, 1968*b*). Similarly, the time taken to digest an item is not considered because this can and does occur simultaneously with the pursuit and swallowing of other prey items for many kinds of predators.

*The final expression*—Combining terms (1), (3), (4), (5), and (6) and dividing by  $C_4B^{1.5}$ , the energy requirements per large period of time, we construct:

$$R_{i,r} = \frac{C_5 i^2 - C_6 B^{1.5}(THS) - C_9 B^{1.5}(TP)}{C_4 B^{1.5}[(THS) + (TP)]}, \quad (7)$$

where  $R_{i,r}$  is that fraction of the predator's total energy requirements contributed by a single item of size  $i$  and distance  $r$  per unit time of pursuit and eating. Note that if we divide by  $C_5$  we can reduce the number of degrees of freedom by one;  $C_5$  is held constant in these simulations and set equal to 10.

#### *Food Abundance Functions*

In all simulations the distribution of food size is assumed log normal. Schoener and Janzen (1968) found that the sizes of arthropods comprising sweep samples from a variety of forest understories are described quite well by a 3-parameter log normal distribution and fairly well by a 2-parameter distribution, the latter producing positive skewness and kurtosis in nearly all cases. Because the increased precision in using a third parameter is slight for these simulations in comparison to the increased complexity in approximating relative prey size abundance, 2-parameter log normal distributions were used here. Approximations were accomplished by subdividing the area over the interval  $(\ln |i - 0.5|, \ln |i + 0.5|)$  into small unit portions for each  $i$  considered, summing values of the density function for the midpoints of these small portions, and then normalizing the results. Most values for the mean,  $\mu$ , and the standard deviation,  $\sigma$ , in  $\log_e[\text{mm}]$ , are taken from real samples (listed in Schoener and Janzen, 1968). If population turnover of small prey is greater than that of large, using these values probably errs in the direction of assuming relatively fewer small insects than actually occur. While limiting the domain of certain numerical results to insectivorous species, so long as these parameters keep their relative values the scale of

predator size can be increased without affecting the simulations.

If  $D_1$  is the total number of prey items (or some fraction thereof) which appear per unit area per large time period, then  $\pi D_1$  is the number of such particles appearing within a circle of unit radius. More generally,  $\pi D_1 (2r_0 - 1)$  is the number of food items appearing within the distance interval bounded by  $r_0$  and  $r_0 - 1$ . In order to calculate the number of items with distance  $r$  from the predator we assume  $r = r_0$ . Actually, mean  $r$  for items within the distance interval upper bounded by  $r_0$ , assuming that all suitably sized items within this interval are taken, is between  $r_0 - 0.5$  and  $r_0$  and approaches the limit  $r_0 = 0.5$  as  $r_0$  increases. The simplification  $r = r_0$  is most valid if  $r$  were measured in very small units or if there were some initial distance which the predator had to traverse no matter where the prey item was located, as would be the case, for example, for an *Anolis* lizard perched on a tree and feeding on the ground.

It should be pointed out here that  $D_1$  ought to be a function of  $T$  for most Type I predators. This is because while feeding, a predator misses a certain fraction of the prey items it is exposed to during the entire activity period, thus lowering the level of available food. In these simulations, the simplifying approximation was made that  $D_1$  is constant for all  $B$ , an approximation which reduces the number of degrees of freedom of the model by two. The approximation is valid if  $T$  for all  $B$  represents a relatively small portion of the total activity period, which is more likely for Type I predators—those which do not spend time searching—than for other types. It is also valid if that fraction of the predator's activity period during which food can be spotted increases proportionately with  $T$ . Indeed, were  $T$  large in relation to the total activity period, rather than insufficient energy being the critical factor for predator viability, insufficient time available for feeding could set this limit.

#### TYPE II PREDATORS

##### *The General Model*

The principal difference between this type of predator and Type I is that while searching for food it utilizes time and energy that is expended for that purpose alone. In most cases this would imply a discrete period of time during which the predator does nothing but forage and eat. Hence, the ideal predator will eat a particular type of food if the energy gained per unit time is greater than the energy gained per unit time by ignoring it and searching for and eating a more favorable item or items. This scheme is incorporated into the contingency equations given by Emlen (1966). For purposes of simplicity, we assume at first that the predator is proceeding through the environment—or otherwise expending energy in its search for prey—and that it uncovers prey items which it can then immediately reach out and swallow without having to first chase the items over an appreciable distance. That is, we assume that the only energy expended by the predator while feeding is that involved in searching and in swallowing or otherwise

handling the prey items as they are encountered. This assumption will be partially relaxed below.

A program was designed which selects that range of food size which enables a predator of a given size to satisfy its energy requirements in the least amount of time, assuming the environment is "fine-grained," that is, that items are encountered in the proportion in which they occur (MacArthur and Wilson, 1967) over some large time period. It is additionally assumed that given an  $N_1$  and  $N_2$ , the lower and upper prey sizes respectively that the predator will eat, all food within the interval  $[N_1, N_2]$  will be eaten. As before, a net energy is calculated for each item for which this value is positive.

If  $E(\epsilon_i)$  is the expected value of the energy gained per item of *available* food, whether taken or not, then

$$E(\epsilon_i) = \sum_{i=N_1}^{N_2} p_i [C_5 i^2 - C_6 B^{1.5} (THS)_i] - C_{10} B^{1.5} (TSE). \quad (8)$$

$THS$ ,  $C_5$ ,  $C_6$ , and  $B$  are defined as for Type I predators,  $TSE$  is the mean search time between items of available food,  $p_i$  is the proportion of food items belonging to class  $i$  for the total food distribution in the environment, and  $C_{10}$  is the cost of searching. If  $E(\epsilon_i) \leq 0$  for all combinations of  $N_1$  and  $N_2$ , the predator is not viable. Otherwise, for any  $N_1$  and  $N_2$ , the number,  $n$ , of available food items necessary for that predator to encounter in order to support itself per large time period should equal  $C_4 B^{1.5} / E(\epsilon_i)$  where  $C_4$  is defined as for a Type I predator. While  $n$  will have some variance due to fluctuations in food abundance or sampling error, this is ignored in the model though in reality it may sometimes be important, particularly for animals which need energy at frequent intervals. The expected handling and swallowing time per item of available food is:

$$E[(THS)_i] = \sum_{i=N_1}^{N_2} p_i (THS)_i.$$

Then the total time taken to handle and swallow all food items for a given feeding period is  $nE[(THS)_i]$  and the total time taken to find all food items is  $n(TSE)$ . Consequently, we wish to minimize  $T$ , the total time spent feeding, where

$$T = n\{E[(THS)_i] + TSE\}. \quad (9)$$

A search procedure was programmed which selects the values of  $N_1$  and  $N_2$  producing the lowest  $T$  for a given  $B$ . As before,  $T$  is calculated for a range of predator sizes and minima are noted.

Mean search time per particle of *available* food,  $TSE$ , is calculated from the expression

$$TSE = \frac{1}{(V'D_2)}, \quad (10)$$

where  $V'$  is the speed with which the predator moves through the environ-

ment and  $D_2$  is the number of available food particles per unit distance. Note that  $D_2$  is *not* necessarily the same value as  $D_1$  for Type I predators, since  $D_1$  is a measure of the number of food particles per unit area per large time period, whereas  $D_2$  measures the number of food particles encountered while moving along a strip of small width representing the search path. We assume here that the strips do not coincide before the prey can completely be renewed: if this is not possible, then insufficient available food may set a limit to predator viability in addition to that associated with equation (8).

The proportion of each food size,  $p_i$ , and calculation of the predator's energy requirements, are as for Type I.

Examples of Type II predators might include such birds as warblers, kinglets, and titmice, as well as lizards such as *Ameiva* and many skinks.

### *Type IIa Predators*

This variety is one of several kinds of searchers which has a prey distance component built into its simulation. Here we assume that distance to any prey item in the area of searching, while substantial, is fairly constant, as would be the case were the predator able to place itself well above the surface of the hunting area rather than on it, as for example, a *Buteo* hawk might be able to do. Now an additional term,  $-C_{11}B^{1.5}(TP)$ , must be added onto equation (8), where  $C_{11}$ , the cost of pursuing, is greater than  $C_{10}$ . The latter may, for this kind of predator, merely be the cost of slowly gliding or sitting on a branch. In this expression,  $TP$  is again  $r/V$ , where  $r$  is now constant, and is incorporated into equation (9). Were the predator *on* the surface of the hunting area,  $r$  would be relatively variable, as is assumed for Type I. Selection of an optimal array of prey items would then become vastly more complicated, since  $E(\epsilon_{i,r})$  would be a function of two variables. This latter kind of searcher was not simulated in this study.

### PREDICTIONS

In the following discussion many consequences of the models will be derived which should be affected little or not at all by irregularities in food-size distributions produced by major competitors. Therefore, it will often be appropriate to test predictions with both solitary and nonsolitary forms.

### *Prey Size Distributions and Home Range*

If for a given  $B$ ,  $R$  is plotted against  $i$  for a variety of distances ( $r = 1, 2 \dots N$ ), families of curves such as those illustrated in Figure 1 are obtained. The procedure of selecting an optimal array of prey items for Type I predators can be visualized as constructing a line (broken in Fig. 1) which parallels the abscissa and passes through that item with the highest  $R$ , and then lowering that line while keeping it horizontal as more and more unfavorable items are added. The lowering stops when enough items are passed through to satisfy the predator's energy requirements, all items above this "demarcation line" comprising the predator's diet. How far the demarcation line must be lowered depends on the quotient  $D_1/C_4$ : the smaller this

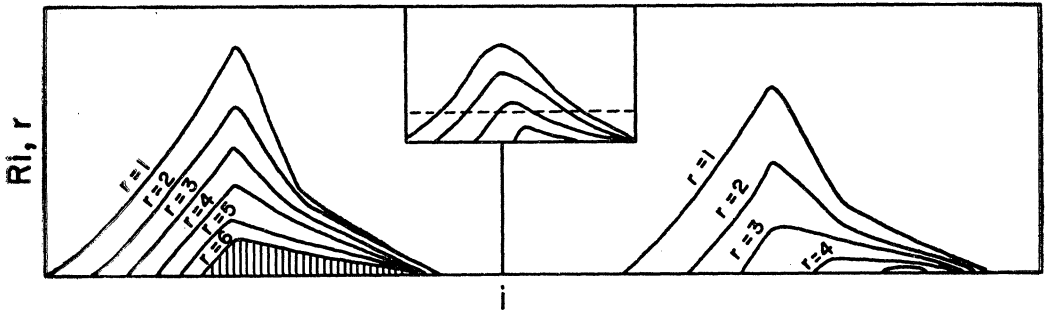


FIG. 1.— $R$  as a function of  $i$  and  $r$ . *Left*: Curves for a predator with a low  $C_0$ . *Right*: Curves for a predator with a high  $C_0$  (curves for  $r > 6$  not shown). *Center*: A possible demarcation line (broken) is drawn in for a hypothetical predator's  $R$ -curves, above which all food items are accepted and below which they are rejected.

value, the further it must drop. Fluctuations in the absolute abundance of food  $D_1$  can be represented as movements of this line up and down on the graph.

A family of  $R$ -curves for a given predator can be tightly packed or very far apart. Predators which lose a large amount of time or energy pursuing prey, such as those with low speeds  $V$  or high costs of pursuing  $C_0$ , should generate a family of curves which are relatively far apart (Fig. 1, right). On the other hand, for efficient pursuers, distance to the prey should not have nearly as much an effect on  $R$  (Fig. 1, left). Consequently, efficient pursuers should take few prey sizes over a wide range of distances, whereas less efficient pursuers of similar energy requirements should take a greater range of food sizes but over smaller distances. Efficient pursuers are much more likely to specialize in mobile prey, so that minimal pursuit distances should be larger in that group. Nearly the same arguments were first advanced by MacArthur and Levins (1964) and later elaborated by MacArthur and Pianka (1966) and Rosenzweig (1966). Apart from the model, less efficient pursuers also should often eat a greater number of kinds of food, that is, be more omnivorous, while efficient pursuers can specialize on foods similar in traits other than size, although then they might expand food-size range. Of course, for a given set of parameters, the greater  $D_1$ , the higher should be the demarcation line and the smaller the maximum distance of reaction to prey. The latter should also be smaller for those animals taking more taxa of food over a given-size range. The radius of the home range, while not necessarily equal to maximum  $r$ , should often vary in parallel with that quantity, especially if home ranges are composed of a constant number of reaction fields. That home-range size fits these predictions about maximum  $r$  has been extensively documented both within and between species (McNab, 1963; Schoener, 1968a).

Fluctuations in  $D_1$  should be partially responsible for variance in home range and food-size range. Furthermore, for efficient pursuers, variance in

home range due to such perturbations should be great relative to that for less efficient pursuers, whereas for the latter predators, variance in prey-size range should be relatively greater. A partial test of this prediction is to contrast *Accipiter* with *Buteo*. While *Accipiter* is rather close to a Type I predator, many buteos might better be considered Type IIa than less efficient Type I pursuers; in either case the prediction should apply, because Type IIa predators are assumed to have a nearly constant  $r$ . In Table 1, that species with the greatest variance in home-range size and the lowest variance in prey-size range is the *Accipiter*. Since the *Buteo* species are all larger, coefficients of variation are more appropriately compared, and these give totally consistent results. *Falco sparverius* has a coefficient intermediate for home range, as might be predicted from its feeding behavior, but has a coefficient slightly larger than expected for food-size range. Mean home range for *Falco* or *Accipiter* is much larger than for the slightly bigger *B. lineatus*, but *Accipiter* has a larger mean prey-size range than does *B. lineatus*. This latter result may be because the number of food items per sample is greater for *Accipiter*, or because that genus is taxonomically more specialized, eating mostly birds.

A second interesting feature of these curves is that for a given increase in  $r$ , change in  $R$  is usually greater for small  $i$  than for larger  $i$ , if both  $i$  are past the maximum. While  $d/di(dR/dr)$  is negative for  $i \leq i_B$ , the change is not very great, and the bigger the  $r$ , the greater the  $i$  at which  $R$  first becomes positive. Furthermore,  $d/di(dR/dr)$  for  $i > i_B$  can be shown to be positive unless  $r$  is very large, so that  $R$ -curves will usually converge at their right tails. These features imply that only relatively large prey are taken at great distances, though the largest prey taken at a given distance will not be as large as the largest taken at smaller distances. Both A. S. Rand (1967); personal communication) and I have many times observed *Anolis* lizards eating miniscule ants which were only a few centimeters from their

TABLE 1

MEAN (M), STANDARD DEVIATION (SD), AND COEFFICIENT OF VARIATION ( $CV = 100SD/M$ ) OF HOME RANGE AND PREY-SIZE RANGE FOR SOME NORTH AMERICAN RAPTORS

SPECIES	BODY WEIGHT	HOME RANGE (sq miles)				PREY-SIZE RANGE (gm)			
	(gm)	N	M	SD	CV	N	M	SD	CV
<i>Buteo lineatus</i> . . . . .	625	37	0.23	0.13	59	27	759	589	78
Michigan									
<i>B. jamaicensis</i> . . . . .	1126	5	1.64	0.35	21	...	...	...	...
Michigan									
<i>B. jamaicensis</i> . . . . .	1126	8	0.73	0.35	48	7	3025	1786	59
Wyoming									
<i>Accipiter cooperi</i> . . . .	470	15	0.77	0.64	83	11	1135	142	13
Michigan									
<i>Falco sparverius</i> . . . .	114	11	0.78	0.50	64	8	84.4	63.2	75
Wyoming									
<i>B. swainsoni</i> . . . . .	988	4	1.12	0.57	51	...	...	...	...
Wyoming									

NOTE.—Calculated from data of Craighead and Craighead (1956). Years combined for Michigan raptors. Food-size range data based on records from separate nests. Each nest considered as one observation. Insects not included.

heads, but long-distance forays in pursuit of prey seem only to be made for large items.

A shifting of  $R$ -curves to the right with increasing  $r$  implies that a predator which must cover extremely large distances to capture prey, as when prey is very mobile, should take prey much larger in proportion to its own size than should less wide-ranging species. This prediction agrees with the tendency for certain *Carnivora* and *Accipiter* hawks to take items very large in proportion to their own bulk. That *Accipiter* take large items relative to *Buteo*, owls, and to a lesser degree the more unspecialized but still wide-ranging falcons, can be seen from a replotting of the data of Craighead and Craighead (1956) by Schoener (1968a, Fig. 6).

In the hundreds of simulations performed, very large predators ate either an equal or a greater range of food sizes than did smaller ones and pursued these prey over the same or a greater range of distances (Fig. 2), although intermediate-sized predators sometimes had wider ranges than did slightly larger ones. Increasing  $D_1$  caused these differences to become less marked. An expanded home range for larger animals has been documented for mammals (McNab, 1963) and birds (Schoener, 1968a), and an expanded prey-size range has been found to hold roughly for certain raptors (Schoener, 1968a) and markedly for *Anolis* lizards (Rand, 1967; Schoener, 1967; Schoener and Gorman, 1968; Schoener, 1968b).

All  $R$ -curves generated with equation (7) have a single peak (although the use of unrealistic values for  $\tau$  and  $\lambda$  can produce two peaks), and the relative slopes of the curve on either side of the maximum are ascertained by taking derivatives of equation (7) with respect to  $i$  for both  $i \leq i_B$  and  $i > i_B$ . This is done in Appendix I and only the principal results will be given here. First, for a given number of sizes greater than  $i_B$  ( $i = B/\alpha + N$  where  $N$  is a positive integer),  $dR/di$  is greater (less negative) the smaller the predator for the sizes closest to  $i_B$ . This means that, since the  $R$ -curves are usually descending past  $i_B$ , the larger the predator the steeper the descent. Indeed, for especially small  $B$ ,  $dR/di$  is positive so that the maximum is well past  $i_B$ , although the maximum rapidly approaches  $i_B$  for increasing  $B$ . Some numerical examples are given in Figure 3. For a given number of sizes less than  $i_B$  ( $i = B/\alpha - N$ ),  $dR/di$  is greater the smaller the  $B$  for the prey sizes closest to  $i_B$ , and for a given  $i$ ,  $dR/di$  increases with decreasing  $B$  so long as for all predators  $i \leq i_B$ . Also, the  $R$ -curves overlap greatly, particularly among the small predator sizes. These features imply that  $R$ -curves for small predators will usually have relatively long tails on the right, whereas those for large predators will usually have relatively long tails on the left.

A result of small predators having their prey sizes of highest yield larger than  $i_B$  is that distributions of prey actually eaten should often be fairly similar below a certain minimum predator size. This prediction is borne out by *Anolis* studies: a plot of average prey size against lizard size for a given species produces a curve which is linearly increasing for most of its length but becomes asymptotic over small lizard sizes (Schoener, 1967; Schoener

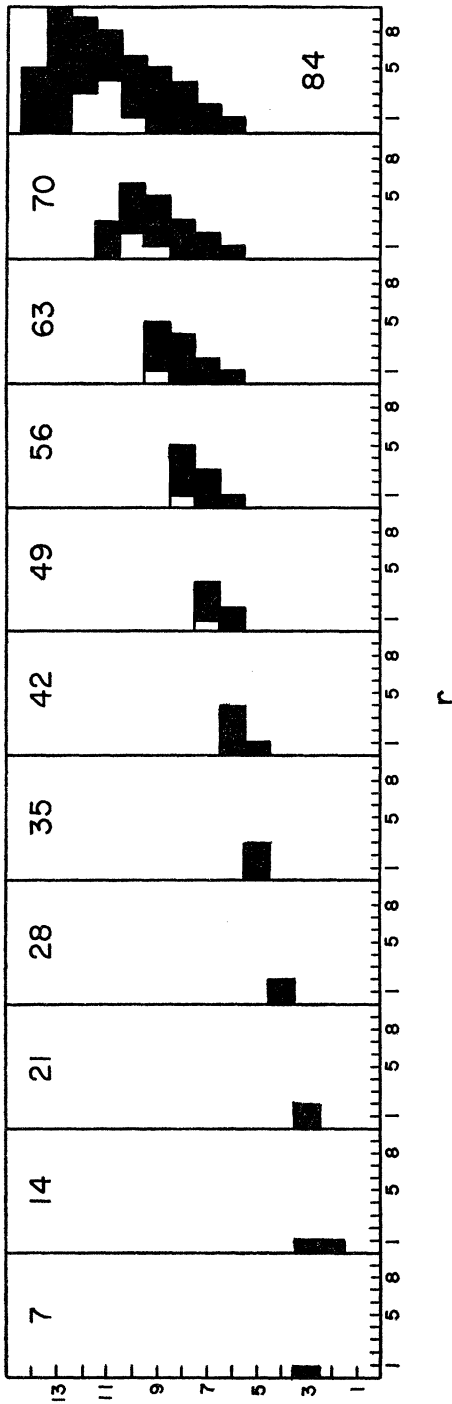


FIG. 2.—A sample numerical result from Type I predator simulation, giving prey size range (ordinate) and prey distance range for each  $i$  (abscissa) for predators of lengths 7–84 at two food densities. Shaded plus clear areas are diets at low food densities ( $D_1 = 1$ ); clear areas only are diets at a higher food density ( $D_1 = 10$ ). The clear areas do not include lowest yield item taken. Parameters used:  $C_0 = 0.1$ ;  $C_7 = 1$ ;  $C_8 = 1$ ;  $C_9 = 1$ ;  $V = 7$ ;  $\mu = 1$ ;  $\sigma = 0.5$ ;  $v = 0$ .



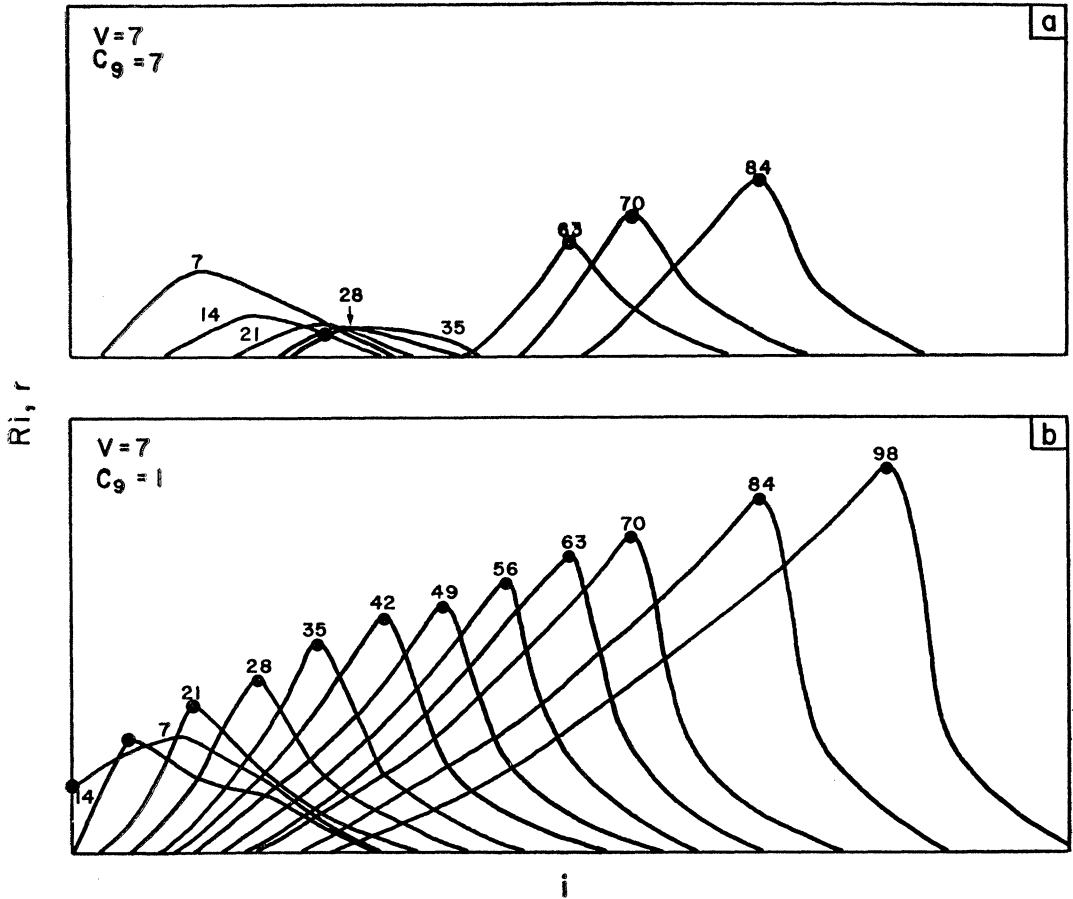


FIG. 3.— $R$ -curves at  $r = 1$  for a range of predator sizes,  $B$ . Predators with curves as in (a) are likely to produce bimodal  $T(B)$  functions; those with curves as in (b) are not. Other parameters:  $C_0 = 0.1$ ;  $C_7 = 1$ ;  $C_8 = 1$ ;  $v = 0$ ;  $\alpha = 7$ . The  $i_B$  is indicated by a dot on the curves (in top graph sizes below 35 have their  $i_B$ 's at negative values of  $R$ ).

and Gorman, 1968; Schoener, 1968b). The explanation previously given (Schoener, 1967), that the very smallest food items taken may be relatively rare, could also contribute to the effect, but even for equinumerous sizes the trend should often hold according to the present model.

By inspection of the expressions for  $dR/di$  (see Appendix I), it is possible to ascertain how changes in other parameters of the  $R$ -curves should affect skewness. Since  $C_9$ , the cost of pursuing, appears only in  $dR/di$  for  $i > i_B$  and is positive, a decrease in this parameter causes the peak of the curve to be displaced to the right. By analogous reasoning, a decrease in  $C_6$ , the cost of handling and swallowing, should have the opposite effect. An increase in  $C_7$  will of course only affect the right-hand portion of the curve

and will usually result in a sharper drop ( $dR/di$  becomes more negative), displacing the peak to the right. An increase in  $C_8$  or  $V$  will change  $dR/di$  for all  $i$  in a direction determined by the values of the other parameters.

Predictions concerning skewness of the  $R$ -curves would not be verifiable in nature unless the abundances of the different prey sizes were known. However, in the laboratory where prey sizes can be made equinumerous, skewness properties can be detected from a knowledge of the relative abundances of the different items in the predator's diet (provided the items are uniformly dispersed). To predict the latter from the model, the range of distances over which the predator accepts food of a given size is noted by counting the number of curves whose  $R$  falls above the demarcation line for each prey size. Considering the fact that the farther the distance interval from the predator, the more food it contains, the relative abundance of an item should increase with the square of the maximum distance over which the item is taken. Since the  $R$ -curves are closer together for large than for small prey sizes, if the  $R$ -curves have long left tails, the distribution of food sizes taken should be even more skewed. Contrarily, if the  $R$ -curves have long right tails, the distribution of food sizes taken by the predator should be relatively more symmetrical, owing to the increase in food availability with the square of its maximum distance. However, the order—left-skewed, symmetrical, right-skewed—or vice versa, predicted for the  $R$ -curves with an increase in the value of a given parameter should not change for diet distributions.

Ivlev's (1961) experiments, in which he presented equinumerous food sizes to fish of varying size and hunting behavior, resulted in curves remarkably like those predicted in this model (compare, for example, his Fig. 21 with Figs. 1 and 3 of this paper). Although the species used were limited, relative symmetry properties of the diet distributions fit well expectations from hypothetical  $R$ -curves. First, he showed that two species of "predatory" fish, pike and perch, having relatively large pursuit components in their feeding behavior, ate prey whose sizes comprised a distribution with the peaks displaced to the right. According to the present model, if efficient pursuers have small  $C_9$ 's they should have relatively steeply descending right portions of their  $R$ -curves. Probably even more applicable, they will take prey over a greater range in  $r$ , resulting in a right-hand displacement of their peaks. Second, he showed that "peaceful" fish—carp, bleak, and bream—whose pursuit component is much less, had either symmetrical diet curves or those with opposite asymmetry to the pursuer's. Finally, the smallest of the three "peaceful" species was the one with the most asymmetrical prey-size curve, having a very long tail on the right, also as predicted likely by the model. Because Ivlev's fish may have been closer to Type II or IIa predators, his experiments are not ideal for testing predictions about changes in parameters for Type I; the same predictions for pursuit components should hold but the effect of  $B$  can be quite variable (see below).

## NUMBER OF RELATIVE MINIMA

Graphs of time spent feeding per large time period  $T$  as a function of predator length  $B$  can have one or several minima. The alternatives are of interest for at least two reasons. First, it is of importance to know whether solitary species should converge to the same size if the trophic variables discussed here were the only important ones. Where such graphs are bimodal, the size distributions of solitary species might also be bimodal, particularly if the ancestral stocks varied greatly in body size and gradients between minima were steep. Second, a bimodal function may indicate that sexual dimorphism in size is favored. It has been hypothesized that dimorphism in size or trophic characters implies that the sexes are utilizing different sets of resources, and hence are avoiding intraspecific competition while increasing the total energy available to the species. A second group of pressures favoring dimorphism for some species is said to be those involved in sexual selection. The literature on these and other possible functions has been recently thoroughly reviewed by Selander (1966; see also Pitelka, 1950; Rand, 1952; Amadon, 1959; Storer, 1966), who convincingly argues for the importance of the first function in many birds. The present model adds still another aspect to a theory of dimorphism, that of individual feeding efficiency. In the absence of competitors, sexes of a species with either a uni- or bimodal plot of  $T(B)$  can feed on largely or entirely non-overlapping resources if food abundance is sufficiently high. But if  $T(B)$  plots were unimodal and gradients steep, one or both of the sexes of a dimorphic species might have to lie well away from the minimum  $T$  in order to avoid considerable resource overlap. Rather than this, it seems more likely that monomorphism will exist, accompanied by one of the spatial modifications suggested by Selander (1966), such as territory enlargement and/or some degree of foraging allopatry. If the plots were bimodal, and the modes were sufficiently far apart, no such adjustment need be made. Thus at the very least, bimodality should facilitate the evolution of dimorphism by adding feeding efficiency to the advantage of resource nonoverlap. Note that considerations of feeding efficiency alone are sufficient to explain the presence or absence of dimorphism in solitary species, something which a theory dealing purely with competing species cannot do. Furthermore, the feasibility of sexual selection could be ascertained by specifying the gradients of a  $T(B)$  plot, for sexual selection cannot push toward sizes whose maintenance would be energetically marginal or impossible.

If a plot of  $T(B)$  produces a single maximum, two relative minima are implied, particularly if the very large or very small predator sizes are non-viable. This is the case for many different simulations using the model for Type I predators (Fig. 4a–g). Most  $T(B)$  curves with  $\alpha = 7$  take a similar form: there is a maximum within the range of  $B$  bounded by 28 and 49. For smaller  $B$ ,  $T$  gradually decreases, reaching a minimum at the smallest  $B$  considered. It is probable that this minimum should not be located here but at slightly larger sizes, since the assumptions made about  $THS$  are

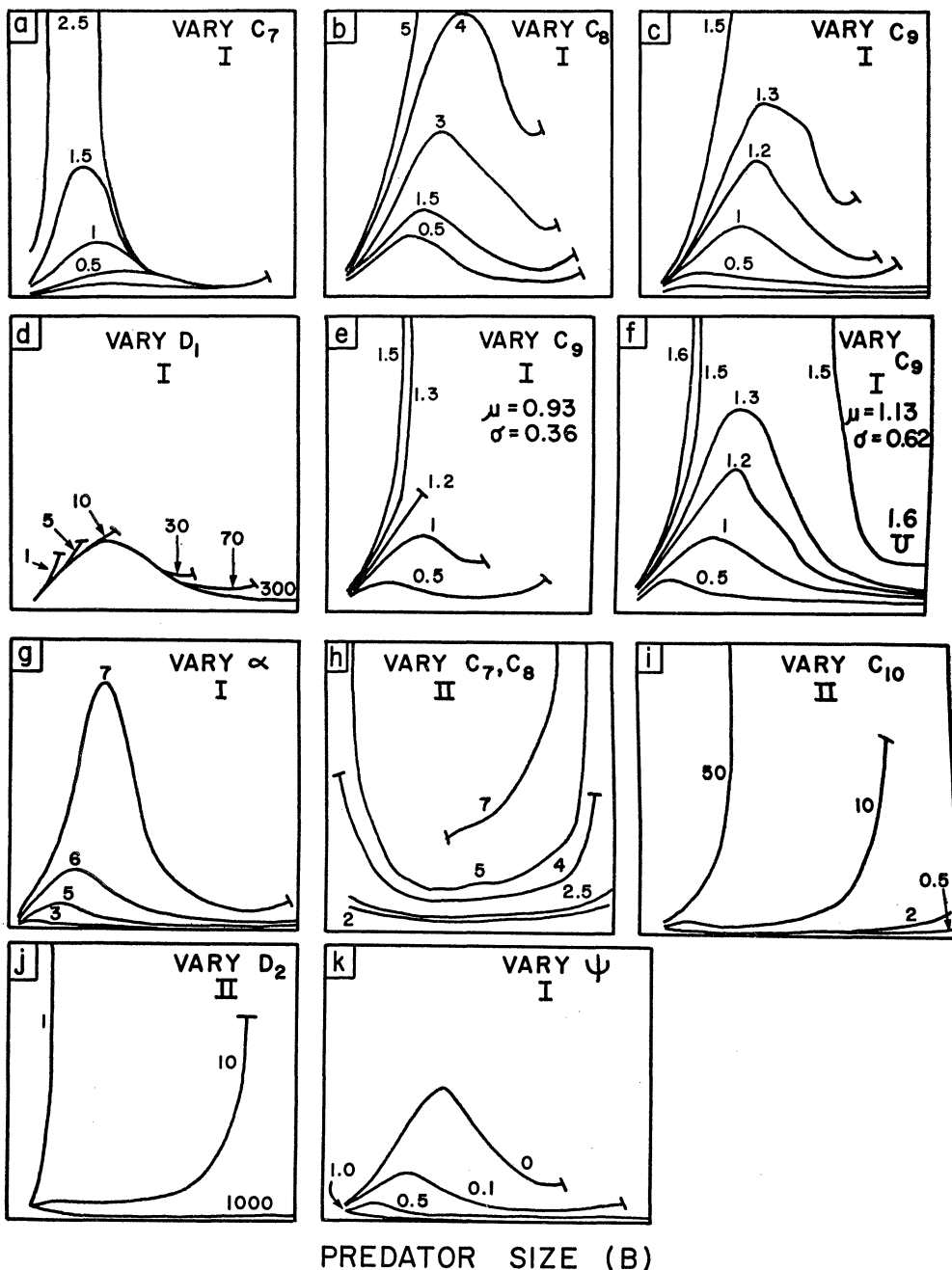


FIG. 4.—The  $T(B)$  plots for Type I (a–g) and II (h–j) predators. A perpendicular line at the end of a curve denotes that predators of the next size simulated are nonviable; were smaller intervals of  $B$  chosen, curves would rise much more steeply before terminating. No simulations were run below  $B = 7$  except those in graph (g). Unless otherwise denoted on the graph, parameter values were:  $C_4 = 1$ ;  $C_6 = 0.1$ ;  $C_7 = 1$ ;  $C_8 = 1$ ;  $C_9 = 1$ ;  $V = 1$ ;  $v = 0$ ;  $D_1 = 100$ ;  $C_{10} = 1$ ;  $\alpha = 7$ ;  $V' = 1$ ;  $\mu = 1$ ;  $\sigma = 0.5$ .

especially unlikely to be true for the smallest  $B$ . If some additional term is added to the expression for  $THS$ , as suggested in a previous section, the curve could be turned up at this end. For  $B$  greater than that producing a maximum, the curve drops to a relative minimum and then turns up again before terminating with a "nonviable" form.

By varying one parameter at a time, it is possible to define some conditions under which a bimodal  $T(B)$  curve can be made unimodal for Type I predators. If  $C_9$  (the cost of pursuing) or  $C_8$  (the "basic" time taken to handle and swallow an item) is increased, cost per item increases more rapidly for large predators than for small, tending to make marginal or nonviable all large  $B$ , including of course that generating the second minimum (Fig. 4b-c). A decrease in  $D_1$ , the absolute density of resources, also causes the second minimum to be eliminated (Fig. 4d). A differential effect on large  $B$  occurs because, for the log normal prey-size distributions used, small food is so much more abundant than large food that small predators, better adapted at eating small prey, are only using a minor portion of the total resources from which they can obtain a positive net energy. Large predators, whose optimal prey sizes are larger, are much closer to utilizing all food from which they can obtain a high net energy. Thus a uniform decrease in food abundance, while affecting small predators only slightly, can have a tremendous effect on the feeding times and viabilities of the larger predators. Since it is the ratio of  $D_1$  to  $C_4$  which controls the relative values of  $T$ , an increase in  $C_4$ , implying an increase in energy requirements, can have the same effect on large sizes as a decrease in  $D_1$ . Changes in the parameters of the log normal prey-size distributions within the range of  $\mu$  and  $\sigma$  actually calculated for insect samples from forest understories can strikingly modify the sensitivity of large sizes toward a decrease in  $D_1$  or an increase in  $C_8$  or  $C_9$ : an increase in either  $\mu$  or  $\sigma$  stabilizes  $T$  for large predators (Fig. 4c,e,f).

An increase in  $C_7$ , that parameter which controls the rate at which  $THS$  increases for  $i > i_B$ , will often eliminate the first minimum before the second (Fig. 4a), since this drastically contracts the range of sizes giving a net positive energy for small predators.

A very different way of changing a bimodal curve into a unimodal one is produced not by adding stresses to the system but by relaxing one. If  $V$ , the speed of the predator, is increased with no proportionate increase in  $C_9$ , a concave  $T(B)$  curve is generated whose minimum is sometimes very near the second minimum produced by simulations using smaller  $V$ 's.

The conditions favoring uni- or bimodality for Type I predators can be partially investigated analytically. Most simulations producing bimodality have  $R$ -curves for the different predator sizes which look roughly like those in Figure 3a. Here, we see that the maximum  $R$  is greater for the smallest  $B$ 's than it is for intermediate  $B$ 's, and that it eventually increases again for the largest  $B$ 's. What is happening is that small predators are utilizing only the very best items because their food is so relatively abundant and consequently  $T$  is smallest for those predators with the highest  $R$ -curves.

Thus at first  $T$  increases with increasing  $B$ . However, once the  $R$ -curves begin to get higher for larger predators,  $T$  begins to decrease again. (Whether or not maximum  $R$  begins to increase again is shown in Appendix II to be dependent upon the relative values of  $\tau_i$ ,  $\tau_B$ , and  $\lambda$ .) Depending on  $D_1$ ,  $\mu$ , and  $\sigma$ , a point is reached at which, in spite of the fact that  $R$ -curves are still increasing in height, food density is so low that many unfavorable items must be utilized, causing an increase in  $T$  until finally there are not enough items to support the predator's energy requirements per large time period. If  $D_1$  is low enough the second decrease in  $T$  will never take place. However, if the  $R$ -curves look as they do in Figure 3b, no such pattern can occur because now intermediate sizes have higher curves than do the smallest predators.

Let us investigate when the maximum  $R$  should be greater for smaller  $B$ 's. Since for small  $B$ ,  $R$  reaches its maximum past  $i_B$ , and for large  $B$  at  $i_B$  (Appendix II), we want to specify the conditions where  $R$  for  $B$  at  $i = M + N + B/\alpha$  is greater than  $R$  for  $B'$  at  $i = N + B'/\alpha$ ,  $B < B'$ ,  $N > 0$  or  $\leq 0$ , and  $M$  such that  $N + M \geq 1$  and  $> N$ . We use the long form of equation (7); if  $N \leq 0$ , all  $C_7 e^N$  terms must be set equal to zero. Expanding, we ask when

$$\begin{aligned} & \frac{C_5 \left( N + M + \frac{B}{\alpha} \right)^2}{B^{1.5} \left( C_7 e^{N+M} + C_8 + \frac{r}{V} \right)} - \frac{C_6 C_8}{C_7 e^{N+M} + C_8 + \frac{r}{V}} - \frac{C_6 C_7 e^{N+M}}{C_7 e^{N+M} + C_8 + \frac{r}{V}} \\ & - \frac{C_9 \frac{r}{V}}{C_7 e^{N+M} + C_8 + \frac{r}{V}} > \frac{C_5 \left( N + \frac{B'}{\alpha} \right)^2}{(B')^{1.5} \left( C_7 e^N + C_8 + \frac{r}{V} \right)} - \frac{C_6 C_8}{C_7 e^N + C_8 + \frac{r}{V}} \\ & - \frac{C_6 C_7 e^N}{C_7 e^N + C_8 + \frac{r}{V}} - \frac{C_9 \frac{r}{V}}{C_7 e^N + C_8 + \frac{r}{V}}. \end{aligned} \quad (11)$$

By inspection, it can be seen that the last term for  $B'$  must be less (more negative) than for  $B$ . The same is true for the second term. Consequently, any tendency to increase the importance of these terms relative to the others will make the inequality more likely to be true. The third term is less (more negative) for  $B$  than for  $B'$ . Hence, any tendency to decrease the importance of this term will favor the inequality. Finally, the status of the first term depends on the values of  $N$ ,  $M$ ,  $B$ ,  $B'$  and  $\alpha$ .

The most effective way to increase the importance of the last term while decreasing that of the others is by increasing pursuit time, that is by increasing  $r$  and/or decreasing  $V$ . This makes the denominators of all terms large but makes only the numerator of the last term large as well, at a rate dependent on  $C_9$ . If  $C_9$  is made small proportionately, no effect on the numerator can be produced. An increase solely in  $C_9$  will have less effect since it is found only in the numerator of one term and in none of the

denominators. An increase in  $C_8$  will cause the denominators of all terms to become large, but only enlarge the numerator of the second term. However, while the direction of the effect is the same as for increasing  $r/V$ , it is much less important, since  $C_6$  should be much smaller than  $C_9$ . A decrease in  $C_7$ , the major term controlling handling time, should decrease the denominators of all terms but decrease the numerator of only the third term, thus favoring the inequality. The effect should be a good bit more marked than with  $C_8$ , because this term has an additional factor,  $e$  to some power  $\geq 0$ .

One final way to reduce the probability of bimodality is to decrease  $\alpha$ , the ratio of  $B$  to  $i_B$  (Fig. 4g). This could be equivalent biologically to increasing the size of a trophic appendage relative to the entire body size. To investigate the effect of changing  $\alpha$ , only the first terms of the above inequality are relevant, and, expanding these terms, we ask for what  $\alpha$

$$\frac{B^{0.5}}{\alpha^2(C_7e^{N+M} + C_8 + r/V)} + \frac{2(N+M)}{\alpha B^{0.5}(C_7e^{N+M} + C_8 + r/V)} \\ + \frac{(N+M)^2}{B^{1.5}(C_7e^{N+M} + C_8 + r/V)} > \frac{(B')^{0.5}}{\alpha^2(C_7e^N + C_8 + r/V)} \\ + \frac{2N}{\alpha(B')^{0.5}(C_7e^N + C_8 + r/V)} + \frac{N^2}{(B')^{1.5}(C_7e^N + C_8 + r/V)}.$$

The last two terms of this expansion can either favor or disfavor the inequality, depending on  $C_7$ ,  $N$ ,  $M$ ,  $B'$ , and  $B$ , but the first term unambiguously disfavors it. The first term will decrease in importance fastest with increasing  $\alpha$ ; hence, the inequality is more likely to be true for large than for small  $\alpha$ .

Type II predators are much less likely to have bimodal curves. When two minima are simulated, they are usually close together and the gradient is much less steep (Fig. 4h-j). Although  $R$ -curves are not computed in Type II simulations, we can specify their form in order to explain the single minimum. Inequality (11) can be adapted to Type II predation if  $C_0$  is replaced by  $C_{10}$  and  $r/V$  is replaced by  $1/(V'D_2F)$ , where  $F$  is the proportion of available food items which the predator will accept. This latter term acts as a kind of buffer, muffling the effects of changes in  $V'$  and  $D_2$ : not only does  $F$  increase with decreasing  $V'$  or  $D_2$ , but it does this differentially with respect to  $B$ . In order to reduce the denominator of this term (and thus favor the inequality)  $V'$  or  $D_2$  must be reduced. But at low  $V'$  or  $D_2$ , rather than at high  $V'$  or  $D_2$ , larger predators have  $F$ 's which are relatively high in comparison with those of smaller predators because at high  $V'$  or  $D_2$  each size can be very particular about what it eats, taking only the best items (which are more abundant in the case of small predators than large predators). This partially cancels the effects of reducing  $V'$  or  $D_2$ . Consequently, very small or "invisible" maxima are produced, mostly close to the smallest  $B$  and often at intermediate values of  $V'$ ,  $D_2$ , or  $C_{10}$ . At very low  $V'$  or  $D_2$ ,  $F$  increases for small  $B$  as well, sometimes to the extent of becoming much

bigger than for large  $B$ . But now, predators with large  $B$  are taking most of their prey from very low-yield items (which are more abundant), and they have very high  $T$ 's or are nonviable. No second minimum can exist under these conditions. Furthermore, Type II predators will generally take a wider range of food sizes than will those of Type I, so that even if  $T(B)$  curves are rather flat, the possibility of overlap in food size is greater for morphs of Type II, again favoring foraging allopatry, except where food is very abundant.

Similar predictions can be made for variation in certain other parameters, with the condition that now gradients are likely to be much less steep: decreasing  $C_8$  and increasing  $C_7$  favor unimodality slightly.

Type IIa predators are somewhat more likely to be dimorphic. The terms

$$\frac{-C_9 \frac{r}{V}}{C_7 e^{N+M} + C_8 + \frac{1}{D_2 V' F} + \frac{r}{V}} \quad \text{and} \quad \frac{-C_9 \frac{r}{V}}{C_7 e^N + C_8 + \frac{1}{D_2 V' F} + \frac{r}{V}}$$

must be added to the left and right sides of the inequality for Type II, and the term  $r/V$  must be added to each denominator. Because the new large terms are more negative for larger  $B$ , the inequality is more likely to hold and will increase in stability with increasing  $r/V$ . As mentioned above, Type IIa is a simplified version of a more complicated predator (Type IIb), in which  $r$  is a variable. Type IIb differs from Type I only in the search component, but the fact that energy is being lost while searching forces it to generalize prey size and distance more if  $C_{10}$  is large and especially if  $V'$  or  $D_2$  are small. Then as  $TSE \rightarrow 0$  and feeding periods become more fragmented, predictions for dimorphism in Type IIb approach those for Type I.

The results can be biologically interpreted as follows:

1. Animals that pursue their prey (Type I) are more likely to be dimorphic than those that search for it (Type II), and the more mobile the prey, the greater the effect. Thus *Accipiter* and *Falco* should be more dimorphic than *Buteo*, but *buteos* should be more dimorphic than warblers. Animals whose ability to handle prey decreases relatively slightly with increasing prey size should be more dimorphic, and this could also explain differences between *Accipiter* and *Buteo*. Owls and kingfishers which are able to judge the size of their prey before pursuit should be dimorphic to the degree that they do not consume a considerable amount of time and energy solely for food search.

2. Those animals which have larger trophic appendages in relation to their size and thus can take larger food because of a decreased  $THS$  are less likely to be dimorphic. Specifically, swallows, goatsuckers, potoos, swifts, and frogs, whether Type I or II predators, should not be as dimorphic as Type I predators with proportionately smaller trophic appendages, such as *Anolis*.

3. Dimorphism of sympatric forms is more likely to be tolerated under conditions of relatively high food density and relatively low energy re-



quirements per predator gram, for two reasons: two minima are more likely to exist and overlap in food size should be less. Low energy requirements imply that poikilotherms, such as lizards and fish, should show dimorphism more frequently than homeotherms of similar size and prey abundances, such as some birds and mammals, a phenomenon true certainly for birds versus lizards on small and isolated islands. The occurrence of sexual dimorphism and its correlation with differential prey size utilization has been discussed for the Goby *Microgobius* (Baird, 1965) and for many species of *Anolis* lizards (Schoener, 1967; Schoener and Gorman, 1968; Schoener, 1968b; Schoener, in preparation). Dimorphism should be especially favored in species whose distributions of prey have a high  $\mu$  and/or  $\sigma$ , such as insectivorous species in tropical seasonal forests. It should be particularly rare in species whose prey distributions have a low  $\mu$  and  $\sigma$ , such as insectivorous species in temperate deciduous-conifer forests (insect data in Schoener and Janzen, 1968).

4. Some species of woodpeckers are among the most dimorphic birds known (Selander and Giller, 1963; Selander, 1966). If prey procurement costs a large amount of time and energy (not related to prey size) relative to the location of that prey, dimorphism might be expected on the same basis as for pursuers as opposed to searchers. But since for some species maximum probing distance or the speed and depth of excavation should be correlated with length of the trophic appendages and perhaps body weight (Davis, 1965), the formulation is more complicated than anything tried above. It should be noted, however, that a significant range of depths over which a woodpecker (or certain members of the Scolopacidae or Rallidae) can obtain prey provides one of the necessary conditions for dimorphism.

All these conclusions are subject to modification once competitors are considered. If the species are separated from one another spatially, most of the arguments remain the same, but if competitors selectively lower a certain portion of the prey abundance distribution, one or the other minimum could easily be displaced or wiped out, possibly shifting the advantage to monomorphism. Selander (1966) has shown that *Centurus* woodpeckers are morphologically more dimorphic in an insular situation than on the mainland and has documented its ecological significance. Even if competitors only result in habitat restriction for the species under consideration, that species could become monomorphic if such restriction resulted in a uniform per cent lowering of food abundance, thus eliminating the second minimum.

### *Position of the Minima*

For Type I predators with two minima, changes in prey abundance (involving  $D_1$ ,  $\mu$ ,  $\sigma$ ) affect the position of the maximum and hence the probable position of the first relative minimum much less than the position of the second relative minimum (contrast especially Figs. 4e and f). This is because, as already mentioned, in these simulations small predators are utilizing a relatively much smaller portion of their possible food items than are

large predators. Therefore, within a group of dimorphic species, the larger the size of the largest sex, the more different it should be from that of the smaller sex. This phenomenon is well documented for solitary *Anolis* lizards (Schoener, in preparation), though it does not hold for the hawk genus *Accipiter* (Storer, 1966). A related idea was suggested by Selander (1966) as a possible explanation for half of Rensch's (1960) empirical rule, the latter being that if the larger sex is male, an increase in size is accompanied by an increase in dimorphism. Corollaries we might expect for predators differing only in size are: (1) More small individuals than large, either of the same or different species, can be fitted into a given area without seriously affecting their energy budgets. (2) Small individuals might be less likely to be food-limited and more likely to be predator-limited, for reasons of food availability as well as susceptibility to predation.

A decrease in either  $D_1$ ,  $\mu$ , or  $\sigma$  can cause a decrease in the optimal size for the largest (or only) morph. Thus species should respond to a uniform reduction in food abundance by changing sizes in the same direction as they would if large food were selectively reduced. A decrease in the energy requirements for a given-sized animal also favors large size, so poikilotherms might be larger than homeotherms (with all the other  $R$ -curve parameters the same) or might be more restricted in the taxonomic variety of food taken. An increase in  $C_9$  will increase the  $B$  with the maximum  $T$  and slightly decrease the position of the second relative minimum (Figs. 4c,e,f). Increasing  $C_8$  has the same effect, only it is much less, because  $C_8$  appears in both the numerator and denominator of equation (7) (Fig. 4b). Both such increases are differentially deleterious to large predators, because  $C_8$  and  $C_9$  are multiplied by a power of predator weight to determine energy loss. On the other hand, an increase in  $C_7$  causes the position of the maximum to shift toward smaller sizes, but has almost no effect on the position of the second relative minimum, because most of the burden of increased energy cost is on the smaller sizes (Fig. 4a).

A decrease in  $\alpha$  shifts the maximum toward smaller  $B$  while causing the gradient to decline markedly (Fig. 4g). If we recall that decreasing  $\alpha$  increases the size of the most profitable items, clearly the second relative minimum (which rapidly becomes the only one detectable) should also shift toward small  $B$ , as the decline in food abundance over large prey sizes becomes more severe. Thus such animals are likely to show only slight dimorphism or none at all.

As  $C_{10}$  increases for Type II predators, the optimal  $B$  decreases. At intermediate values of  $C_{10}$ , a slight peak often appears, very close to the smallest  $B$ , which then vanishes as  $C_{10}$  continues to increase (Fig. 4i). A slight peak appears in similar locations for intermediate values of  $D_2$  or  $V'$  (Fig. 4j). Where peaks appear elsewhere, they are always very small and usually at intermediate values of the relevant parameters. Arguments for why this should be so are given above. Hence Type II predators when dimorphic should often be more similar in size than Type I predators, provided diet overlap does not counter the effect.

A test of these ideas is readily available: dimorphism in *Accipiter* and *Falco*, more nearly Type I predators, is greater than that in *Buteo*, more nearly Type IIa predators (Table 2).

As  $C_4$ ,  $C_7$ ,  $C_8$ ,  $C_9$ ,  $C_{10}$ , and  $C_{11}$  are increased, gradients of the  $T(B)$  plots become steeper, whereas a decrease in  $V$ ,  $D_1$ , or  $D_2$  has the same effect (Fig. 4). These results are unsurprising, but it would be useful to measure gradients empirically so as to assess the likelihood of predators existing at their minima. Where other major selective pressures (sexual selection, climatic factors, predator avoidance) favor large size, a gentle gradient could increase the expectation that species be at sizes larger than those with a minimum  $T$ . Any change in the gradient, as might be produced by a decrease in food abundance, could cause a predator's size to evolve toward that with a minimum  $T$ , tipping the balance of selective forces in the direction favored by feeding efficiency.

#### ALTERNATIVE TYPE I PREDATORS

Up to this point it has been assumed that the speeds of predator and prey,  $V$  and  $v$ , are not functions of their sizes. Let us now ask what are the consequences of relaxing one or both these assumptions, that is, of letting  $V = V_B B^\psi$  and  $v = V_B B^\phi$ . In order to expand the list of possible predators even more, and for the sake of logical completeness, some of the properties of predators whose  $THS$  is not a function of predator or prey size will also be discussed. Each of the three terms— $V$ ,  $v$ , and  $THS$ —can either be con-

TABLE 2  
SEXUAL DIMORPHISM IN SIZE OF WING AND BILL FOR FALCONIFORMES

Species	N Males : Females	Wing Length ♀ (mm)	Wing ♀ / Wing ♂	Bill Length ♀ / Bill Length ♂
<i>Accipiter striatus striatus</i> * . . .	5 : 6	182	1.22	1.26
<i>A. s. velox</i> . . . . .	51 : 40	200	1.17	1.23
<i>A. cooperi</i> . . . . .	34 : 27	260	1.13	1.17
<i>A. gentilis atricapillus</i> . . . . .	27 : 22	334	1.03	1.08
<i>Falco sparverius sparverius</i> . . .	64 : 68	195	1.06	1.04
<i>F. s. dominicensis</i> * . . . . .	16 : 13	183	1.03	1.04
<i>F. columbarius columbarius</i> . . .	28 : 32	208	1.10	1.14
<i>F. albicularis albicularis</i> . . . .	11 : 18	220	1.16	1.15
<i>F. tinnunculus tinnunculus</i> . . .	7 : 5	252	1.04	1.16
<i>F. femoralis femoralis</i> . . . . .	11 : 7	271	1.12	1.16
<i>F. mexicanus</i> . . . . .	17 : 18	343	1.14	1.18
<i>F. peregrinus anatum</i> . . . . .	20 : 22	356	1.13	1.19
<i>F. rusticolus obsoletus</i> . . . . .	42 : 59	403	1.11	1.11
<i>Buteo jamaicensis calurus</i> . . . .	37 : 45	411	1.06	1.08
<i>B. j. jamaicensis</i> * . . . . .	5 : 6	366	1.09	1.08
<i>B. albonotatus</i> . . . . .	7 : 9	420	1.08	1.12
<i>B. lineatus lineatus</i> . . . . .	26 : 22	339	1.06	1.07
<i>B. swainsoni</i> . . . . .	20 : 38	405	1.05	1.07
<i>B. platypterus platypterus</i> . . . .	17 : 17	283	1.08	1.06
<i>B. lagopus s.-johannis</i> . . . . .	22 : 9	411	1.01	1.03
<i>B. magnirostris griseocauda</i> . . .	11 : 4	243	1.06	1.03
<i>B. nitidus micrus</i> . . . . .	25 : 21	265	1.10	1.09
<i>B. galapagoensis</i> * . . . . .	22 : 15	388	1.09	1.13

NOTE.—Adapted from Selander (1966) with additional data from Friedmann (1950).  
\* Insular form.

sidered functions of  $B$ ,  $i$  or both terms respectively, or can be treated as constants. The two possible states of each term taken three times produce eight kinds of predators, some vastly more realistic than others.

Three of these are of no interest in the present study, since it can be verified by substituting the appropriate values into equations (2), (3), and (7) that in their cases no optimization problem with respect to size exists. If all three of the terms are constants or if only  $v$  is a function, it is always best to be small. If only  $V$  is a function, it is also always best to be small, provided  $\lambda \geq \psi$ , which from the available evidence seems to be true (see above).

The two next most complex cases are in one sense exact opposites. The first, in which  $THS$  is a function of  $i$  and  $B$  but  $TP$  is a function of neither, is the case we have been discussing above. It is possible to create an alternate model in which larger predators prefer larger prey solely because they are better at capturing the relatively faster large prey, rather than because they are better at handling or swallowing it as in the original Type I. In this case,  $V$  and  $v$  are functions of  $B$  and  $i$ , respectively, but  $THS$  (set =  $C_8$ ) is independent of both. Three of the major predictions which are changed in this case are:

1. Inspection of  $d/di(dR/dr)$  plus computer simulation indicate that  $R$ -curves are more likely to converge greatly below their maxima with decreasing  $i$ . This implies that an increase in the initial distance over which predators pursue their prey ( $r$ ) usually should not involve as great an increase in average prey size.

2. Animals with relatively large  $C_9$ 's should have the peaks of their  $R$ -curves displaced to the right, not those with low  $C_9$ 's, as in the original case.

3. Changes in  $C_9$  and those factors affecting the pursuit time ( $r$ ,  $V_B$ ,  $V_i$ ,  $\psi$ ,  $\theta$ ) now have the opposite effect on the probability of producing two modes, although changes in  $C_8$  have the same effect. However, two modes are much less likely than in the opposite case because the major term favoring bimodality is one in which  $C_8$  is a factor rather than  $C_9$  as before.

Though far from conclusively incorrect, these predictions seem to correspond less well with existing information. Also, since a completely invariant  $THS$  is almost inconceivable, this case is probably not very common in nature, if it occurs at all.

More likely are cases in which  $THS$  and one or both speeds are functions of size. As might be imagined, the effects of changes in a given parameter are often not monotonic but are dependent upon the values of the other parameters. An example of modifying the original Type I predator by setting  $V = V_B B^\psi$  is given in Figure 4*k*. Note that as  $\psi$  increases, a bimodal distribution becomes unimodal. As can be checked by comparing the appropriate form of inequality (11), an increase in  $\psi$  can disfavor dimorphism by reversing the relative values of the last terms on either side of the inequality sign or by making these terms insignificant in value in comparison with the others. If the latter be true, then a decrease in  $V_B$ , by

increasing the relative value of this term, can still reverse the effect (just as a decrease in  $V$  can do in the original case), something which would not be true were relative values reversed.

These exercises indicate that it is important to be as exact as possible in specifying the type of organism being considered, and if the only good models are too complex, many qualitative predictions from energetics are not a priori invariant but can only be made so after empirical determination of certain parameters.

Unlike Type I predators, the effect of making speed, in this case the search speed of the predator  $V'$ , a function of  $B$  is to reinforce the tendency towards unimodality found in the simpler case, rendering it even more likely that searchers will be monomorphic.

#### CHARACTER DISPLACEMENT AND CONVERGENCE

Although the conclusions so far have dealt mainly with solitary species, it is possible to suggest consequences of those invading species which affect the shape or level of distributions of available prey. MacArthur and Wilson (1967) have recently presented a model for discrete resources in which convergence or divergence is possible between competing species depending on their degree of specialization and food abundance (see also MacArthur and Levins, 1967). Using an altogether different approach, we recall that the more absolute food abundance is reduced, the more optimal predator size shifts toward small  $B$ . This suggests that if an invading competitor is generalized enough with respect to prey size to lower food abundance by a more or less uniform factor, the resident species should become smaller, *even if the invading species is initially smaller than the resident species*. The invader should also decrease in size. On the other hand, for specialized species, food abundance will be selectively lowered over sizes corresponding to those predated upon by the invading species. Consequently, classical character displacement should occur, smaller invaders now causing the resident species to become larger and vice versa.

The degree of change will depend on food abundance in two ways. As shown above, the larger  $D_1$ , the less any change in  $D_1$  will affect the optimal size. Thus character displacement *or* partial convergence due to invading species is least likely where food is very abundant. Recall also that for most simulations, particularly those in which  $T(B)$  curves are bimodal, small predators consumed relatively less of their possible food than did large predators. Therefore, the addition of competing species should have less effect on the sizes of small species than on those of large species in the same area, provided small species are not correspondingly more dense. Furthermore, a lesser change in small species implies that since both species become smaller, the net result is a smaller interspecific difference than the initial one. In dimorphic species, the size of the smaller sex should be relatively less changed by competitors than that of the larger sex.

But there is a second way in which density affects predictions about changes in optimal size. As shown in the simulations, the lower  $D_1$  or  $D_2$ ,

the greater the range of food items taken. Hence, species are likely to be more generalized with respect to food size in situations of food scarcity, thus implying greater likelihood of both species becoming smaller after overlap. In situations of higher food abundance, change in size, if it takes place, is more likely to occur along conventional paths.

Certain species of lizards which are organized so as to have many different size classes in overlapping habitats should be particularly generalized as a whole with respect to prey size, and any adult sexual dimorphism will intensify this effect. Consequently, the sizes of such species in the presence of sympatric similar species should be less than when solitary. This pattern has indeed been discovered by Soulé (1966) for *Uta* on the islands off Baja California and found also by Schoener (in press) for several species of *Anolis* inhabiting certain West Indian archipelagos. Birds, on the other hand, attaining maturity rather quickly, are more specialized in food size as a whole and are more likely to show classical character displacement. That birds may sometimes be affected in the same way as lizards is suggested by the reported "small island effect," in which the largest forms sometimes occur on relatively small islands (Rand and Rabor, 1960); Grant (1965), however, found the opposite trend for the Tres Mariás Islands.

Finally, it should be noted that invasion by competitors may force the resident species to expand the range of food sizes eaten, whereas in the absence of competition, a species may be allowed to contract that range, taking only the very best items. Hence, the important aspect of the tendency for certain birds species to have longer bills (often in proportion to their mass) on islands than on mainlands, amply documented by Grant (1965), may sometimes be that they are able to take larger prey in proportion to their energy requirements rather than a greater range of prey sizes. Disproportionate increase in bill length could be equivalent to decreasing  $\alpha$  and results in a smaller  $T$  for the same  $D_1$  (Fig. 4j). A greater opportunity for shifting to larger prey on small islands for some species may have existed if large-prey specialists, which are relatively wide-ranging, were filtered out of restricted insular situations.

MacArthur and Pianka (1966), using a different approach, have concluded that in the presence of a competitor, species should initially shrink habitat but not, conspicuously, diet. Likewise, for the types of predators considered here, a decrease in food abundance, as might be caused by a competing species, results in an expanded or unchanged range of items eaten. However, those species with newly expanded diets will usually no longer have optimal phenotypes, so that selection will favor either a change in size or a reduction of interspecific spatial overlap, or what seems most likely, some combination. Which will predominate will depend in some as yet quantitatively unspecified way on the genetic, physiological, and ecological feasibility of the two. Some hypotheses as to these feasibilities are given by Schoener (1965). Species compression acted upon by natural selection will undoubtedly take place by both contraction and shift in habitat and

shift (at least) in range of prey size, in contrast to packing purely by the first mechanism, proposed by MacArthur and Wilson (1967) for very short-term situations.

#### CONCLUSION

This model differs from three recent major models of predation—those of Holling (1966), MacArthur and Pianka (1966), and Emlen (1966)—in that it considers sizes of the predator and prey as variables. Holling's model is more specific, simulating a real predator-prey interaction sequence, in which one predator species and one prey size are used. MacArthur and Pianka's and Emlen's models are more general, allowing food items to vary in ways other than size and without specifying particular functions to describe this variation.

Models, such as the present one, which are both hypothetical and complex attempt to ply the channel between the Scylla of unsubstantiated assumption and the Charybdis of limitless plasticity. But there are advantages in this approach, too, which may partially justify its use. The construction of a composite function such as that for  $R$  from several simpler functions rather than, for example, assuming that  $R$  can be described by one or a family of very simple functions, allows one to list a greater number of plausible ways of arriving at the same predictions. While even qualitative falsification is then sometimes difficult or impossible, the specificity of the model should often suggest which parameters need to be empirically determined in order to insure a proper test. Furthermore, attempts to specify these simpler functions and parameters provide a mapping of the patchiness of certain areas of ecological knowledge. Where gaps exist (as for example in the function for  $THS$ ), I have been forced to make the simplest possible assumptions in order to complete the model. That the model, built from relatively few monotonic and unimodal functions, is able to produce a number of new and nonobvious hypotheses, such as those concerning bimodality, will provide, I hope, motivation and direction toward gathering data which supply the missing information.

#### SUMMARY

Models are presented which predict an optimal size, defined as that size which takes the least amount of time to satisfy its energy requirements, for several types of predators: I—predators which expend no time or energy in food search alone and which pursue their prey over varying distances; II—predators which expend time and energy while searching for items but none in pursuit; IIa and IIb—predators which expend time and energy both in search and pursuit. All predators are assumed to expend time and energy in handling and swallowing prey. In the simplest models considered, equations are constructed which combine to produce three major properties: (a) larger predators expend more energy in pursuing an item over a given distance than do smaller ones; (b) for most prey items, larger animals expend less time and for somewhat fewer items less energy in

handling and swallowing than do smaller predators; (c) time and to a lesser extent energy lost while searching between two items are often not very different for differently sized predators, but to a large degree are homeostatically controlled by varying the range of acceptable items. The kinds of predictions and how these vary with parameters describing feeding efficiency and size-abundance distributions of available prey are summarized for these simple models in Table 3. Some of the ways in which more complicated models, produced by varying the above three properties, might change these predictions are specified.

Several of the more interesting predictions consistent with existing data are (examples in parentheses) :

1. For the same-sized predators, variance in home-range size should be greater in animals which are efficient pursuers (*Accipiter*) than less efficient pursuers (*Buteo*), whereas variance in food-size range should be greatest for the latter group.

2. As predators (*Anolis* lizards) become smaller, size distributions of prey consumed should become more and more similar, until a further decrease in size involves no further reduction in average prey size, even if available prey sizes are equinumerous.

3. Predators (*Accipiter*, some *Carnivora*) which pursue their prey over large distances should eat a mean prey-size larger in comparison with their own bulk than should less wide-ranging predators.

4. Distributions of prey sizes eaten by predators from a uniform size-abundance distribution of available prey should be more negatively skewed if the predator pursues its prey over greater distances (perch, pike) or

TABLE 3  
EFFECT OF INCREASING VARIOUS PARAMETERS ON SOME PROPERTIES OF  $T(B)$  FUNCTIONS  
(IF  $V$  OR  $v$  ARE NOT FUNCTIONS OF  $B$  OR  $i$ ).

Parameter	$N$ Visible Relative Minima*	Position of Only or 2d Relative Minimum†	Position of Relative Maximum	Gradient
$C_4$ ...	S, L $\rightarrow$ S(I)	-(I)	0(or -) (I)	+
$C_6$ ...	Depends on $C_7, C_8$	Depends on $C_7, C_8$	Depends on $C_7, C_8$	+
$C_9$ or $C_{11}$ ...	S, L $\rightarrow$ S	-	+	+
$C_{10}$ ...	L $\rightarrow$ S, L $\rightarrow$ S	-	...	+
$C_8$ ...	S, L $\rightarrow$ S(I)	-	+	+
$C_7$ ...	S, L $\rightarrow$ L(I)	0 or +	-	+
$V$ or $1/r$ ...	S, L $\rightarrow$ L	+	-	-
$V'$ ...	S $\rightarrow$ S, L $\rightarrow$ L	+	...	-
$v$ ...	L $\rightarrow$ S, L	-	+	+
$D_1$ or $D_2$ ...	S $\rightarrow$ S, L(I)	+	0 (or +) (I)	-
	S $\rightarrow$ S, L $\rightarrow$ L(II)			
$\mu$ ...	S $\rightarrow$ S, L(I)	+	0 (or +) (I)	-
$\sigma$ ...	S $\rightarrow$ S, L(I)	+	0 (or +) (I)	-
$\alpha$ ...	M $\rightarrow$ S, L(I)	+	+	+
Type I....	Usually 2	Far from 1st	Far from S	...
Type II ...	Usually 1	Close to 1st	(Close to S)	...
Type IIa...	Usually 1(2)	Close to 1st	(Close to S)	...

\* S, M, and L denote relative minima which are at small, intermediate or large values of  $B$  respectively, I and II denote predators of Type I and II.  
† +, -, and 0 indicate that the only or second relative minimum shifts to larger  $B$ , shifts to smaller  $B$ , or undergoes no change, respectively.



is relatively large than if the predator pursues its prey less (carp, bleak, bream) or is relatively small.

5. Animals which spend a large portion of their feeding time pursuing (*Accipiter*, *Falco*) should more often be markedly sexually dimorphic in size than those which do not (warblers and to a lesser degree *Buteo*).

6. Small insectivorous poikilotherms (*Anolis*) should more often be markedly sexually dimorphic in size when solitary than small insectivorous homeotherms (flycatchers).

7. Rather than classical character displacement, a lowering of the sizes of both resident and invading species (*Anolis*, *Uta*) should occur, even if the invader is smaller than the resident, if species are generalized with respect to food size or if food is relatively scarce.

8. The degree of sexual dimorphism in size (*Anolis*) and size difference between species (many birds) should often be greater the larger the species.

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#### APPENDIX I

In this appendix derivatives with respect to  $i$  are taken for both parts of the function specifying  $R$ , and inequalities are constructed to compare these derivatives for different  $B$ .

1. For  $i > i_n$ ,

$$\frac{dR}{di} = \left[ \left( \frac{r}{V} + C_8 + C_7 e^{i-B/\alpha} \right) (2iC_5 - C_6 B^{1.5} C_7 e^{i-B/\alpha}) - (C_7 e^{i-B/\alpha}) \cdot \left( C_5 i^2 - C_6 B^{1.5} C_8 - C_6 C_7 B^{1.5} e^{i-B/\alpha} - C_6 r \frac{B^{1.5}}{V} \right) \right] / \left[ C_4 B^{1.5} \left( \frac{r}{V} + C_8 + C_7 e^{i-B/\alpha} \right)^2 \right].$$

This can be rewritten:

$$\frac{C_7 e^{i-B/\alpha} (C_9 - C_6) \frac{r}{V}}{C_4 \left( C_7 e^{i-B/\alpha} + C_8 + \frac{r}{V} \right)^2} \quad (a)$$

$$+ \frac{2iC_5}{C_4 B^{1.5} \left( C_7 e^{i-B/\alpha} + C_8 + \frac{r}{V} \right)} \quad (b)$$

$$-\frac{C_5 i^2 C_7 e^{i-B/\alpha}}{C_4 B^{1.5} \left( C_7 e^{i-B/\alpha} + C_8 + \frac{r}{V} \right)^2}. \quad (c)$$

We wish to investigate when  $dR/di$  at  $i = B'/\alpha + N < dR/di$  at  $i = B/\alpha + N$  if  $B' > B$ ,  $N > 0$ . At these values, term (a) is constant; terms (b) and (c) can be rewritten, eliminating the common factor  $C_5/[C_4(Ce^N + C_8 + r/V)]$ ,

$$\frac{2}{\alpha B^{0.5}} \left[ 1 - \frac{C_7 e^N N}{C_7 e^N + C_8 + \frac{r}{V}} \right] \quad (d)$$

$$+ \frac{N}{B^{1.5}} \left[ 2 - \frac{C_7 e^N N}{C_7 e^N + C_8 + \frac{r}{V}} \right] \quad (e)$$

$$- \frac{B^{0.5}}{\alpha^2} \left[ \frac{C_7 e^N}{C_7 e^N + C_8 + \frac{r}{V}} \right]. \quad (f)$$

Term (f) is always more negative for  $B'$  than  $B$ . For  $N$  small enough, terms (d) and (e) are positive and hence smaller for  $B'$  than  $B$ . Therefore, for the  $i$  values closest to  $i_b$ ,  $R$  will decrease more rapidly past  $i_b$  for  $B'$  than  $B$ .

2. For  $i \leq i_b$ ,

$$\frac{dR}{di} = \frac{2C_5 i}{C_4 B^{1.5} \left( C_8 + \frac{r}{V} \right)}.$$

If  $B' > B$ , we ask under what conditions  $dR/di$  at  $i = B'/\alpha - N < dR/di$  at  $i = B/\alpha - N$ , or substituting and eliminating common factors, when

$$\frac{1}{\alpha(B')^{0.5}} - \frac{N}{(B')^{1.5}} < \frac{1}{\alpha B^{0.5}} - \frac{N}{B^{1.5}}.$$

Although the first terms favor the inequality, the second terms do not. But for  $N$  small enough, the second terms cannot change the direction of the inequality. Hence for  $i$  values close to  $i_b$ ,  $i \leq i_b$ ,  $R$  will increase less rapidly with  $i$  for  $B'$  than  $B$ .

Sections (1) and (2) imply that  $R$ -curves for large  $B$  should usually be more negatively skewed than for small  $B$ , because the preferred items and those with positive energy yields are at or adjacent to  $i_b$ . An increase in  $\alpha$  will lessen the effect.

## APPENDIX II

We first show that there exists a  $B_0$  such that for all  $B > B_0$ ,  $R$  reaches its maximum at  $i_b = B/\alpha$ . For all  $B$ ,  $R$  at  $i = B/\alpha$  is greater than  $R$  at  $i = B/\alpha - N$ . Thus we need only to compare  $R$  at  $i = B/\alpha$  with  $R$  at  $i = B/\alpha + N$  and for  $\tau_1 = 2$  to ascertain when

$$\left[ \frac{C_5 B^{2-\lambda}}{\alpha^2} - C_6 C_8 - C_9 \frac{r}{V} \right] \left[ \frac{1}{C_8 + \frac{r}{V}} \right] \\ > \left[ C_5 \left( \frac{B^{2-\lambda}}{\alpha^2} + \frac{2N}{\alpha B^{\lambda-1}} + \frac{N^2}{B^2} \right) - C_6 C_8 - C_9 \frac{r}{V} - C_6 C_7 e^N \right] \left[ \frac{1}{C_8 + C_7 e^N + \frac{r}{V}} \right].$$

If  $B$  is large enough this is true and remains true for increasing  $B$  and positive  $R$  provided  $2 \geq \lambda > 1$ . Analogously, it can be shown that if  $\tau_i = 3$ , the same holds, but now provided  $3 \geq \lambda > 2$ . Both these conditions on  $\lambda$  are reasonable if  $\tau_i = \tau_B$ , since then they require that  $1 \geq \phi > 0.5$  or  $1 \geq \phi > 0.67$  respectively. Using equation (7) for  $i = B/\alpha$ ,

$$\frac{d}{dB} = \frac{C_5}{C_8 + \frac{r}{V}} \left[ B^{\tau_i-1-\lambda} \left( \frac{\tau_i - \lambda}{\alpha^{\tau_i}} \right) \right].$$

This number is positive as long as  $\tau_i > \lambda$ , so for all  $B' > B > B_0$ , there exists at least one, and possibly more values of  $R$  which are larger than any values of  $R$  for  $B$ . We can also specify the behavior of  $R$  at  $i = B/\alpha + N$ . The relevant derivative is

$$\frac{d}{dB} = \frac{C_5}{C_8 + C_7 e^N + \frac{r}{V}} \left[ \left( \frac{B}{\alpha} + N \right)^{\tau_i-1} B^{-\lambda} \left( \frac{\tau_i - \lambda}{\alpha} - \frac{N\lambda}{B} \right) \right].$$

This number is always positive if  $(\tau_i - \lambda) / \alpha > N\lambda/B$ . Since  $N\lambda/B$  monotonically approaches the limit zero as  $B$  increases, there is some  $B_1$  such that for all  $B > B_1$ , the derivative is positive provided  $\tau_i > \lambda$ . Thus for all units of  $i$  past  $i_B$ , values of  $R$  will increase with  $B$  for  $B$  large enough;  $\tau_i > \lambda$  if  $\tau_i = \tau_B$  since  $\lambda = \phi\tau_B$ , where  $\phi < 1$ .

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