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Dimensionless invariants from foraging theory's marginal value theorem

(dung flies/insect mating systems/sperm competition/phenotypic plasticity/patchy environment)

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ABSTRACT Copula duration (t) decreases, and proportional rate of sperm transfer (c) increases, with larger male body size in dung flies, so their dimensionless product ($c \cdot t$) is approximately constant (≈ 2.2). The most recent copulating male fertilizes about 89% of the eggs laid ($= 1 - e^{-c \cdot t} = 1 - e^{-2.2}$), independent of his body size. The conditions under which natural selection favors this phenotypic invariance are studied with fitness optimization models. The dimensionless rules for optimal patch residence times are then generalized to cover phenotypic variation in other foraging cases.

Optimization models, both frequency-dependent and -independent, have been widely and successfully used in evolutionary ecology to predict the attributes of organisms [see Parker and Maynard Smith (1), Charnov (2), and Stephens and Krebs (3)]; most such models maximize fitness (or its proxy) in the face of tradeoffs and constraints. The present paper uses an optimization approach to explore some general patterns in the use of a patchy environment. In particular, we seek general rules for a phenotypic version of the marginal value theorem or MVT [see Charnov (4) and Parker and Stuart (5)], a theorem that has been widely used in behavioral ecology to predict when a solitary forager should abandon a particular resource to begin searching for a new one. Two important features in the MVT are subject to phenotypic variation: (i) the travel time taken to find a new resource after quitting the existing one, and (ii) the rate at which gains accrue while exploiting a given resource. These effects are likely to be inversely correlated because, compared with the average, a "good" forager is likely to have a lower travel time and a higher rate of resource gain than a "bad" forager. We seek rules relating optimal exploitation times to between-individual variation in these two features of patch use. We also seek general rules for how variation in patch quality may affect MVT solutions. Although our modeling efforts will focus on the specific problem of copula duration in dung flies, which provided the empirical puzzle, the marginal value rules should apply to optimal patch duration times in a wide variety of foraging cases.

Copula Duration in Dung Flies

The reproductive behavior of dung flies, *Scatophaga stercoraria*, has been widely analyzed by using ideal free (6–8) and marginal value models (5) in behavioral ecology. Dung fly males arrive quickly at fresh cattle droppings and capture and copulate with incoming gravid females, which arrive more slowly. Females usually contain sperm from previous matings (9) and as copulation occurs, new sperm gradually displace previously stored sperm at a decreasing rate (10). After copulation, the male guards the female while she oviposits in the

dropping, thereby ensuring that his sperm are not displaced. By allowing a male to mate, the female gains not only sperm but also the benefits of the male's postcopulatory guarding phase—she avoids harassment from searching males while she oviposits in the dropping (11).

The topic of this paper was stimulated by data in Fig. 1, where copula duration (t) is plotted versus male body size (H = the cube of hind tibia length). The hatched line is a linear regression through the data; the curve formed by the open dots gives the copula duration expected if a male sets t to maximize the number of eggs he fertilizes per unit time while around the dropping. The optimal copula duration is quite close to the observed except for very small males ($H < \approx 20 \text{ mm}^3$; ref. 12). We will explain shortly how the prediction of optimal t was made. To explain the meaning of the heavy continuous curve through the filled circles in Fig. 1, which fall essentially on top of (within 10% of) the predicted relation, first we must explain the mechanism of sperm competition in dung flies: Seminal fluid flows out from the male at a constant rate and displaces an equal volume of fluid from the female's sperm stores; there is immediate mixing of sperm store contents (5, 10). This process generates an expected gain curve $G(t)$ which shows exponentially decreasing fertilization returns (5).

$$G(t) = G_m[1 - \exp(-c \cdot t)], \quad [1]$$

where c = the proportionate rate of sperm displacement, defining the rate at which $G(t)$ rises to its asymptote, and G_m equals the total number of eggs the female will lay.

Note also that Eq. 1 is the general expectation of cumulative prey gains with time for a randomly searching predator from a patch in which there are initially G_m prey items at time $t = 0$, and where c is the constant proportionate rate at which prey are captured.

c has units of time^{-1} , so the product $c \cdot t$ is dimensionless. The heavy continuous line in Fig. 1 represents the copula duration size relation associated with the dimensionless invariant $c \cdot t = 2.2$; because c increases with male body size (12) t must decrease to hold their product a constant. Referring again to Eq. 1, we note that $c \cdot t$ invariance implies that the guarding male will fertilize about 89% ($= 1 - e^{-2.2}$) of the female's eggs, independent of his body size. Fig. 2 illustrates this independence in a set of laboratory experiments using small to medium-sized males ($H < 37 \text{ mm}^3$).

Here we use MVT optimization models for copula duration to explore the surprising fact that copula duration (proportional fertilization) appears to satisfy an invariance principle. We will explore a series of models of increasing complexity, our goal being to ask two questions: What meaning can be attached to the invariance of $c \cdot t$, and how broadly might the invariance rule apply?

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Abbreviation: MVT, marginal value theorem.

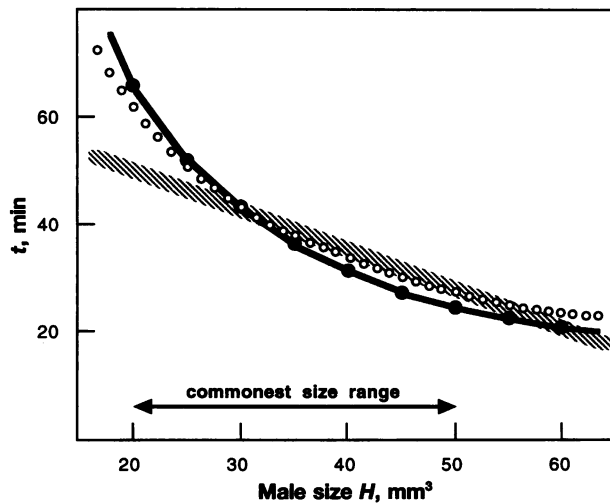


FIG. 1. Relationship between copula duration t (in min) and male size H [hind tibia length (in mm) cubed] in dung flies. Hatched line is the observed relationship, which has $t = 65.38 - 0.74H$ (see figure 4A of ref. 12 for details and statistics). The heavy line with filled circles shows the t^* calculated on the assumption of invariance of $c \cdot t$ by taking the mean value for $c = 0.062 \text{ min}^{-1}$ [average of a series of data sets of Parker and Simmons (10)] and the mean value for t as 35.5 min (5, 6). Thus $c \cdot t \approx 2.2$, and since c increases with H as $c = -0.003 + 0.0018H$ (see figure 2 of ref. 12 for details and statistics), t^* is calculated as $2.2/c$. The open circles give the exact t^* predicted from Eq. 5, with $c \cdot \mu$ derived as follows. The value of $c(H)$ is calculated from the regression equation above. $\mu(H)$ is estimated as follows. From field data, it takes on average 156.5 min to find and guard a newly arriving female (6), and all earlier calculations of the optimal copula duration were based on this value. However, this value for μ should be reduced because of takeovers, an effect which increases with male size, H . The method of calculation of the effect of takeovers on μ is fully explained by Parker and Simmons (figure 3b of ref. 12). The predicted curve for t^* calculated from substituting $c(H) \cdot \mu(H)$ into Eq. 5 is slightly closer to the observed t^* than $c \cdot t$ invariant prediction, but not greatly so. Note that both predictions give a good fit over the commonest size range (only approximately 10% of paired males are smaller than $H = 20 \text{ mm}^3$, and 10% are larger than $H = 50 \text{ mm}^3$). The fit breaks down only for very small males [the predicted curves move out of the 95% confidence limits about the observed t below approximately $H < 17 \text{ mm}^3$; see Parker and Simmons (12)].

Phenotype and Patch Variation

We next evaluate a number of models framed, for clarity, in dung fly terms, but which have generality across many examples of foraging (for either food or mates). In reality, natural conditions typically consist of a phenotype distribution of foraging abilities (“good” and “bad” foragers) and a distribution of resource qualities (“good” and “bad” patches). The models examine the two sources of variation separately and then in combination. All are potentially plausible because an optimal strategy depends on the information available to, and the assessment potential of, a forager. For example, an individual may “know” its relative foraging ability (for a male dung fly, this relates to his own body size) but may not be able to assess the quality of the resource patches (for a male dung fly, this relates to female body size—i.e., the size of the female with whom he is mating). The models to be explored (with their more general equivalents in parenthesis) are as follows:

- (i) One male size and one female size (one type of forager and one type of patch)
- (ii) Many male sizes and one female size (many types of forager and one type of patch)
- (iii) Many male sizes and many female sizes (many types of forager and many types of patch)

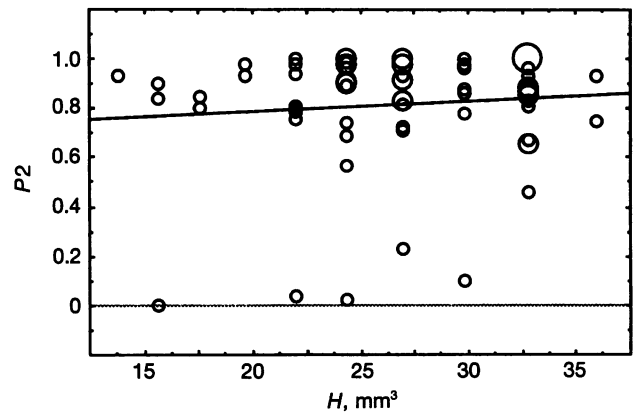


FIG. 2. Proportion of eggs fertilized by the second male to mate (P_2), in the clutch laid after the second mating, remains constant and independent of male body size (measured as H , the cube of male hind tibia length); the area of each symbol is proportional to the number of data points at that location. The slope of the regression of P_2 against H is not significantly different from zero (sample size = 70, $F_{1, 68} = 0.59$, $P = 0.45$). Virgin females were reared in the laboratory and then mated to two virgin males, one of which had been irradiated so that the P_2 value could be determined from the proportion of eggs which failed to hatch. Both males were allowed to mate until natural separation, and male hind tibia length was recorded. [For details of the techniques see Simmons and Parker (13)].

(iv) One male size and many female sizes (one type of forager and many types of patch).

One Male Size and One Female Size (One Type of Forager and One Type of Patch). Consider a system with a single forager phenotype and a single patch type. The male dung fly’s fertilization gains, G , depend on how long (time t) he has copulated—i.e., on how much of his sperm relative to previous sperm is present in the female’s sperm stores. Calling μ the mean time to find and guard an incoming female, the eggs fertilized by the male per unit time on the dropping are given by

$$\frac{\text{eggs fertilized per female}}{\text{time to find and guard one female} + \text{copula time per female}} \text{ or } \frac{G(t)}{\mu + t} \tag{2}$$

The optimal time to copulate (t^*) may be found by setting $d(\text{Eq. 2})/dt = 0$. This t^* result satisfies the MVT: a male should leave when his marginal gains from mating drop to the expected gain rate from the habitat as a whole. t^* is shown graphically in Fig. 3. Formally, this solution is where

$$\frac{dG(t^*)}{dt} = \frac{G(t^*)}{\mu + t^*} \tag{3}$$

Note that increasing μ increases t^* .

With $G(t)$ given by Eq. 1, $dG(t)/dt = G_m \cdot c \cdot \exp(-c \cdot t)$; substituting this and Eq. 1 into Eq. 3 yields

$$\exp(c \cdot t^*) = c(\mu + t^*) + 1, \tag{4}$$

from which t^* readily can be iterated numerically. Hence G_m does not affect optimal copula duration t^* , which depends only on μ and c ; indeed, $c \cdot t^*$ is solely a function of $c \cdot \mu$ (14).

Since Eq. 4 is implicit in t^* , it is a bit awkward to work with. Stephens and Dunbar (14) show that, provided $c \cdot \mu > 2$, the following explicit form gives an excellent approximation to Eq. 4:

$$c \cdot t^* \approx \left(\frac{c \cdot \mu + 2}{c \cdot \mu + 1} \right) \ln(c \cdot \mu + 1). \quad [5]$$

Earlier analyses of optimal copula duration in dung flies (5, 9), which, aggregated (averaged over) male and female size classes, showed that the mean observed copula duration of 35.5 min was quantitatively close to that predicted by Eq. 5: 41.4 min. The mean displacement rate $c = 0.062$ (10)—i.e., roughly 1/16 of stored sperm are displaced per minute of copulation; and overall, from field estimates, average $\mu = 156.5$ min (6). The $c \cdot \mu$ of 9.8 puts $c \cdot t^*$ equal to 2.6 (from Eq. 5); the observed value is $35.5 \times 0.062 = 2.20$, an 18% difference. This estimate of average μ is undoubtedly too large because it ignores females lost or gained through takeovers; recent estimates using the frequency distributions of male size and the estimated $\mu(H)$ relation from Parker and Simmons (12) (Fig. 4) give an average $\mu \approx 120$ min when takeovers are included. This new estimate makes $c \cdot \mu \approx 7.3$ and $c \cdot t^* \approx 2.4$, even closer to the observed. But Fig. 1 says that $c \cdot t^* \approx 2.2$ over a wide range of male body sizes, not just as an average; we take this up next.

Many Male Sizes and One Female Size (Many Types of Forager and One Type of Patch). In this model there is one patch type (with the same G_m for all foragers), but foragers differ in their foraging abilities and can vary their optimal t accordingly. Explicitly, where foraging ability increases with an aspect of phenotype, H , we expect both μ and c to be functions of H , and we seek the optimal response across phenotype, $t^*(H)$. From Eq. 5, it is clear that if the product $c(H) \cdot \mu(H)$ is approximately constant with H then $c(H) \cdot t^*(H)$ must remain constant, and so the optimal t^* must decline as c increases. An obvious way for this to apply is that good foragers have reduced travel times and higher resource gain rate, and that, as a rough approximation, travel time decreases inversely with H and resource gain rates increases directly with H : $\mu(H) \approx k_1/H$; $c(H) \approx k_2 H$. Then the product $c(H) \cdot \mu(H)$ is approximately constant as $k_1 \cdot k_2$.

For dung flies, Parker and Simmons (12) have applied the argument of Fig. 2 (Eq. 2 leading to result 5) to males of various body sizes, producing the curve described by open circles in Fig. 1. They also observed copula duration, t , in lab experiments, using males of known size mated to females of random size (189 matings), so that t could be estimated as a function of male body size H . The essentials of their data are as follows (Fig. 4). As male body size increases: (i) travel time μ decreases because all males have similar prospects of capturing newly arriving females, but large males are better able to gain females

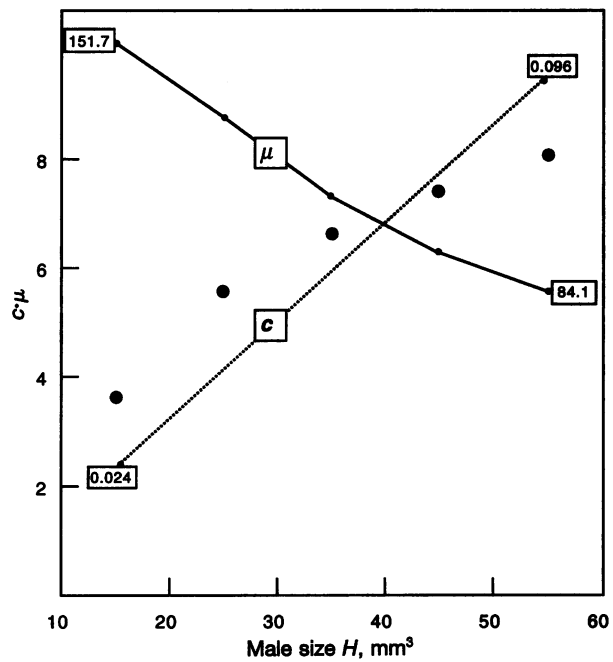


FIG. 4. The large dots give the relationship between $c \cdot \mu$ and male size H (hind tibia length cubed). The solid line with smaller dots gives the value for μ from the estimates of Parker and Simmons (figure 3b of ref. 12), and the dotted line gives the value of $c = -0.003 + 0.0018H$ (see figure 2 of ref. 12 for details and statistics). The limit values for lines μ and c are indicated in boxes; the scales are linear within these limits.

by takeovers; (ii) sperm displacement rate c increases because larger males transfer sperm to females at a faster rate [$c(H) = -0.003 + 0.0018H$]. Thus, increasing male body size results in a decrease in μ and an increase in c . The end result, putting these effects into Eq. 5, is that t^* decreases as body size increases (open circles of Fig. 1).

But Fig. 1 shows that the calculations of Parker and Simmons fit the invariance result $c \cdot t^* \approx 2.2$ reasonably well. Eq. 5 says that $c \cdot t^*$ will be constant if $c \cdot \mu$ is constant. But $c \cdot \mu$ will be approximately constant because c and μ change in opposite directions with changes in male body size (Fig. 4). Or at least $c \cdot \mu$ appears constant enough for $c \cdot t^*$ to always be near 2.2. To see this note that $c \cdot \mu$, for male body sizes $H > 20 \text{ mm}^3$, is in the range 4.5–9, a 2-fold variation (Fig. 4). The first term on the right-hand side of Eq. 5 is in the narrow range 1.2–1.1, while the second (ln) term on the right is always in the range 1.7–2.3. The terms go in opposite directions as $c \cdot \mu$ doubles from 4.5 to 9, so their product ($c \cdot t^*$) varies only from about 2 to 2.5; a 2 × change in $c \cdot \mu$ results in only about a 0.25 × increase in the predicted $c \cdot t^*$. The $c \cdot t^*$ number is thus rather insensitive to this variation in $c \cdot \mu$, and stays near 2.2. Thus the reasons $c \cdot t^*$ is approximately a constant with male body size are, first, that c and μ go in opposite directions (Fig. 4) so their product varies little and, second, that for $c \cdot \mu$ above 4, $c \cdot t^*$ increases very slowly with $c \cdot \mu$ (see figure 1 in ref. 14). The observed variation in $c \cdot \mu$ is small enough for a fixed central value of $c \cdot \mu$ to fit the data (Fig. 1) rather well (excepting for small males).

Constant proportional fertilization ($1 - e^{-c \cdot t}$) is an alternative way to view this invariance (Fig. 2). Fig. 5 illustrates the MVT for two male sizes ($H = 25$ and 50 mm^3) in the face of a single female size. The large male has small μ and a steeply rising $G(t)$ curve, whereas a small male has the reverse. The MVT answers yield quite different t^* values but almost identical predicted proportional fertilization.

Many Male Sizes and Many Female Sizes (Many Types of Forager and Many Types of Patch). The previous model allowed male size (forager phenotype) to vary but treated fe-

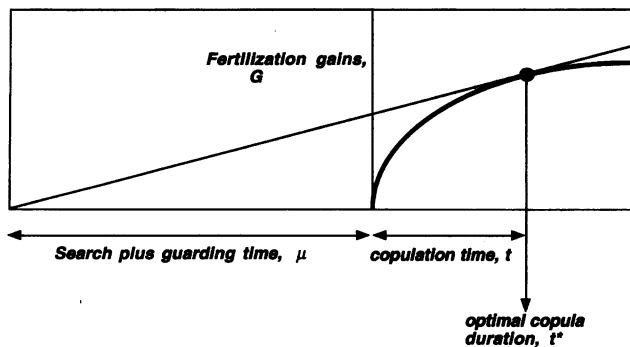


FIG. 3. Graphical MVT solution for a forager in a habitat with just one patch type. The forager takes time μ to find a resource patch and stays in the patch for time t^* . The cumulative gain, G , increases monotonically with decreasing returns with time t spent in the patch. At t^* , the gradient of $G(t)$ is equal to the tangent slope $G(t)/[\mu + t]$. For dung flies, G is the proportion of the eggs about to be laid that will be sired by the copulating male, μ is the time taken to find a female and to guard her during the oviposition which will follow mating, and t is the copulation time.

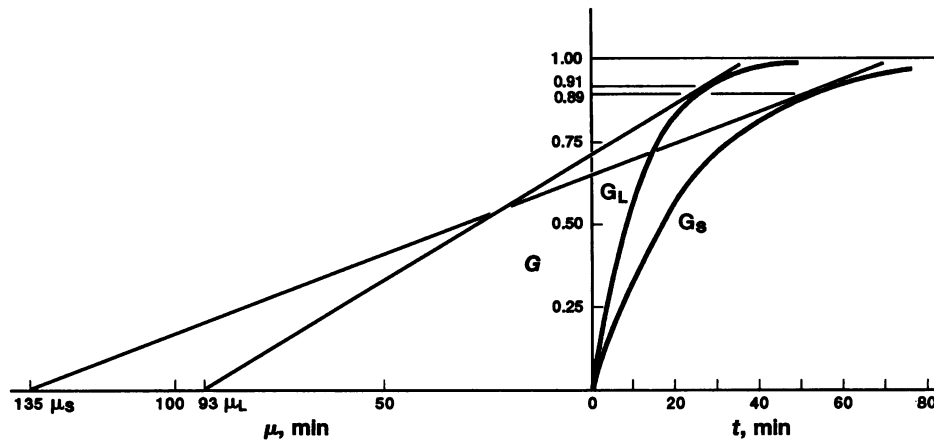


FIG. 5. $c \cdot t$ invariance across male sizes means that the proportional fertilization ($1 - e^{-c \cdot t}$) is independent of male size. This figure shows the MVT predictions for a small (s) ($H = 25 \text{ mm}^3$) and a large (L) ($H = 50 \text{ mm}^3$) male in an environment with a single female size (one G_m). The μ (135 and 93 min) and c (0.042 and 0.087 min^{-1}) values used are from Fig. 4 and lead (by Eq. 5) to predicted $c \cdot t$ values of 2.18 (small) and 2.45 (large). These make $G = 1 - e^{-c \cdot t} \approx 0.9$ for both male sizes. Fig. 1 shows that the observed t values are very close to the values implied here.

males (patch type) as being of a single size; a more realistic assumption would be to allow female size to vary also. The Parker and Simmons (12) experiments to estimate c and t randomized female sizes for each male size and then used averages of t and c (denoted \bar{t}, \bar{c}) over the females to produce the data plotted in Figs. 1, 2, 4, and 5. Here we use the multipatch (multi-female-size) version of the MVT to ask for conditions that result in $\bar{c} \cdot \bar{t}^*$ to be invariant over male sizes for a fixed distribution of female sizes. Except for one special case, developed in the following section, $c \cdot t^*$ is not predicted to be invariant over female sizes (patch types).

Suppose that females come in discrete size categories, with f_i the proportion of size i (actually f_i is the proportion of size i encountered by our focal sized male). Each female size (at a fixed male size) has an associated G_{m_i}, c_i , and t_i ; the time to find and guard one female is again μ . For a focal male size, the number of eggs fertilized per unit time while around the dropping satisfies the multifemale (multipatch) rate equation (4)

$$\frac{\text{average fertilizations}}{\text{time}} = \frac{\sum_i f_i \cdot G_{m_i} (1 - e^{-c_i t_i})}{\mu + \sum_i f_i t_i} \quad [6]$$

The optimal copulation times ($t_j^*, j = 1, 2, \dots$) are where the $\partial(\text{Eq. 6})/\partial t_j = 0$ for all j (4) or

$$\frac{\sum_i f_i \cdot G_{m_i} (1 - e^{-c_i t_i^*})}{\mu + \sum_i f_i t_i^*} = G_{m_j} \cdot c_j \cdot \exp(-c_j t_j^*) \quad [7]$$

Eq. 7 is less formidable than it looks because the left-hand side is the average fertilizations per unit time while on the dropping, whereas the right-hand side is the marginal gains while with a female of size j . Eq. 7 is unchanged if we multiply through by $1/\bar{c}$, resulting in the following for our focal male size:

$$\frac{\sum_i f_i \cdot G_{m_i} (1 - e^{-c_i t_i^*})}{\mu \cdot \bar{c} + \bar{c} \cdot \sum_i f_i t_i^*} = G_{m_j} \cdot \frac{c_j}{\bar{c}} \cdot \exp(-c_j t_j^*) \quad [8]$$

Now consider a second sized male (denoted by $'$), who encounters the same size distribution of females. Suppose he transfers sperm at a different rate; then all of his c values will

equal a constant (h) times the first sized male's c values (see below): $c'_i = h \cdot c_i$. Note that this applies across all female sizes, so that $\bar{c}' = h \cdot \bar{c}$; thus c_i/\bar{c} is independent of male size. Suppose further that MVT for the second sized male produces $c'_i \cdot t'^*_i = c_i \cdot t^*_i + \Delta_i$; we thus have $(t'^*_i = c_i \cdot t^*_i + \Delta_i)/h \cdot c_i$ and can write Eq. 8 for female j for the second sized male.

$$\frac{\sum_i f_i \cdot G_{m_i} (1 - e^{-c'_i t'^*_i} e^{-\Delta_i})}{\mu' \cdot \bar{c}' + h \cdot \bar{c} \cdot \sum_i f_i \left(\frac{c_i t^*_i + \Delta_i}{h \cdot c_i} \right)} = G_{m_j} \cdot \frac{c_j}{\bar{c}} \cdot e^{-c_j t^*_j} e^{-\Delta_j} \quad [9]$$

Provided that again phenotype affects μ and c in compensatory fashion so that $\mu \cdot \bar{c} = \mu' \cdot \bar{c}'$, the only solution in Eq. 9 is for $\Delta_i = 0$ for all female sizes, for the $c_i \cdot t^*_i$ to be invariant with male size. It then follows that $E(c \cdot t^*)$ and $\bar{c} \cdot \bar{t}^*$ are invariants over male sizes (where E and overbar mean average). To show that all $\Delta = 0$ in Eq. 9, note that (if $\bar{c} \cdot \mu = \bar{c}' \cdot \mu'$) Eq. 9 is the same equation as Eq. 8 with the t^*_i in Eq. 8 changed to $t^*_i + \Delta_i/c_i$. But we already know that the t^*_i in Eq. 8 are the only ones that satisfy it; thus $\Delta_i \neq 0$ cannot satisfy the equality.

The condition that $\bar{c} \cdot \mu$ be invariant with male size is the multi-female-size (multi-patch-type) analogue to the Eq. 5 requirement of $c \cdot \mu$ invariance discussed previously; good foragers have lower μ but higher c so that $c \cdot \mu$ tends to stay constant across phenotypes differing in foraging ability. Indeed, for dung flies, Fig. 4 plots \bar{c} and μ versus male body size and shows the approximate invariance of their product. $\bar{c} \cdot \bar{t}^*$ is likewise just as insensitive to changes in $\bar{c} \cdot \mu$ as was $c \cdot t^*$ to changes in $c \cdot \mu$ (previous calculations).

Furthermore, in dung flies, the c_i values for each type of female should change proportionally with male size (i.e., $c'_i = h \cdot c_i$) provided the main influence on the c_i as a function of male size is simply the rate at which the male transfers sperm. If the sperm transfer rate (s) is a function of only male size and decreases with male size, then so should c_i , which equals s/S_j for a female with a displacement vessel (bursa or spermatheca) holding a maximum of S_j sperm. This of course makes $\bar{c} = s \cdot E(1/S)$; males encountering the same size distribution of females share the same $E(1/S)$. Thus a male's \bar{c} will be proportional to his sperm transfer rate (s), resulting in a decrease of \bar{c} with decreasing male size. Because the takeover effect makes μ increase with decreasing male size, their product ($\bar{c} \cdot \mu$) is approximately constant (Fig. 4).

One more interpretation exists for $c \cdot t^*$ invariance across male (predator) sizes. Eqs. 8 and 9 tell us that $\bar{c} \cdot \mu$ invariance implies $c \cdot t^*$ invariance across males at each and every female (patch) size. Because the gain from an encounter with a female

(patch) of size i is $G_m(1 - e^{-c_i t_i^*})$, the gain in eggs fertilized from i is the same for all males independent of the male's size.

$c_i t_i^*$ Invariance over Female Sizes (for a Single Male Size)?
In the last section we noted that, in general, $c_i t_i^*$ is *not* expected to be the same for each female size (at a fixed male size). However, one special condition does lead to $c_i t_i^*$ invariance over female sizes (patch types). We do not know if these special conditions are met in dung flies (but see below), but we develop the case anyway because we think the conditions may be rather common for other kinds of foragers. We couch our discussion in more general foraging terms.

Consider a system in which individuals do not vary in their foraging abilities, but resource patches vary. More specifically, the patch area varies, but the initial density of prey items per unit area of patch, before exploitation, is constant across all patches. For this case, the cumulative gain from a patch i rises to its asymptotic value, G_m , where all the prey are captured, following Eq. 1 (G_m is the total prey in i). c_i is the proportionate rate of prey capture of a focal forager in patch type i . The forager searches at a fixed speed, so we can let $c_i = g/G_m$, where g = a constant relating to the capture rate at initial prey density for the focal forager. Because g is constant for a given forager across patch types i, j , c_i must decline with G_m ; bigger patches have lower c_i . In hypothetical dung fly terms, males mate with females of many sizes and bigger females carry more eggs (6, 11) and are hence analogous to bigger patches (they have higher G_m). Also, because of the mechanism of sperm competition, if bigger females have larger vessels in which sperm displacement occurs (the site of displacement is not yet known, but is likely to be either the bursa or the spermatheca), then they are likely to have a lower proportionate rate of sperm displacement c_i by a given male (12).

From MVT Eq. 7 we know that equalization of marginal gains across female sizes means that for females of any sizes k and j :

$$G_{m_j} c_j \exp(-c_j t_j^*) = G_{m_k} c_k \exp(-c_k t_k^*) = \text{Eq. 7.} \quad [10]$$

Eq. 10 contains the information we need to ask how $c_i t_i^*$ varies across female sizes for a fixed male size.

Suppose we wish to have $c_i t_i^*$ a constant, independent of female size. This can happen either if G_m and c are each (effectively) constant with female size, or their product is a constant (i.e., they are inversely proportional). If $c_i G_m = g$, then Eq. 10 reduces to $g \exp(-c_j t_j^*) = g \exp(-c_k t_k^*)$, and the g cancels so that $c_i t_i^*$ must be the same for all female sizes.

Why *might* c and G_m be inversely proportional? One possible hypothesis for dung flies, mentioned above, is that a female's egg count (G_m) and displacement vessel volume (S) both are proportional to her body weight (or $G_m = rS$). If the focal sized male transfers sperm to any size female at rate s , then $c = s/S \propto G_m^{-1}$ with proportionality constant s/r . However, the data presently available (L. W. Simmons and G.A.P., unpublished data) suggest that female size does not influence t , so if S_i changes across females as just suggested, males either cannot or do not assess this and change their t^* accordingly. Further studies are necessary to estimate S as a function of female size.

A world characterized by $G_m c$ a constant across various patch types (female sizes) has a distinctive signature. For this constancy to apply, we require initial foraging rates to be equal across patch types, since $dG(t)/dt \rightarrow G_m c$ as $t \rightarrow 0$; perhaps this signature would be easily recognizable by a typical forager (if not a male dung fly).

Conclusion

This paper has developed an invariance approach to use of a patchy environment, motivated by some intriguing empirical results for copulation duration in dung flies (Figs. 1 and 2). These results may apply much more generally to patchy environments characterized by MVT solutions for movement rules.

We believe that $c_i t_i^*$ should be a constant across predator sizes (for the same collection of patches) because if movement rate is a function of predator size, individuals with slower movement rates should have longer interpatch travel times (μ) and smaller c values. This should be sufficient to make $c \mu$ approximately a constant over predator size for a specified set of patches; the MVT (Eqs. 8 and 9) then makes $c_i t_i^*$ an invariant across predator sizes. Of course, the stronger result is that $c_i t_i^*$ is invariant across predator sizes for *each and every* patch type i .

The gain curves $G(t)$ for a great many "foraging in a patchy environment" situations can be approximated by the negative exponential function $G(t) = G_m[1 - \exp(-c t)]$. Eq. 10 says that a forager facing an environment with several kind of patches should make $c_i t_i^*$ a constant across the patch types if $c \propto G_m^{-1}$. This may often be approximately true, particularly if G_m is primarily controlled by the physical size of the patch (with initial resource densities roughly equivalent across patch types) and the predator's search rate is independent of patch size. Larger patches should have larger G_m values but smaller c values because c is the proportional rate at which the patch is searched.

Dimensionless invariance has provided interesting insights into other evolutionary problems, particularly life histories (15, 16). To the best of our knowledge, the present paper is the first use of such thinking in foraging theory, and the first attempt (along with ref. 12) to find general rules for use of a patchy environment in the face of phenotypic variation in foraging abilities.

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