Animal Behaviour 108 (2015) 175–182

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Switching tactics: phenotypic plasticity in the alternative mate-finding tactics of burying beetles

Tess E. P. Mulrey, Anne-Katrin Eggert, Scott K. Sakaluk*

School of Biological Sciences, Illinois State University, Normal, IL, U.S.A.

ARTICLE INFO

Article history:
Received 4 May 2015
Initial acceptance 3 June 2015
Final acceptance 3 July 2015
Available online 25 August 2015
MS. number: A15-00368

Keywords:
alternative mating tactic
burying beetle
conditional strategy
Nicrophorus orbicollis
phenotypic plasticity
pheromone
signalling

Male *Nicrophorus* burying beetles utilize two alternative mate-finding tactics: searching and signalling. The searching tactic involves flying in search of a carcass on which to mate, while the signalling tactic involves emitting pheromone in the absence of a carcass to attract females. All males use both tactics, but the amount of time spent using each tactic differs between individuals. Because all males are phenotypically plastic in the time spent using alternative behaviours, the expression is likely to be condition dependent on some environmental cue, such as the availability of reproductive resources (i.e. females and carcasses). We tested how the expression of alternative tactics is influenced by previous mating experience and the perceived availability of females versus carcasses by using a repeated measures design in which mate-finding behaviour of males was observed before and after exposure to: (1) multiple females but no carcasses, (2) multiple females and multiple carcasses, (3) multiple carcasses but no females, or (4) no females or carcasses (control). Males in the multiple-female group (but lacking a carcass) allocated significantly more time to signalling, as did males in the control group lacking both mating and carcass experience. Thus, males that did not encounter carcasses during the treatment period increased pheromone emission thereafter. In the two groups that were given carcasses, however, investment in signalling was not altered. With respect to time allocated to searching, control, multiple-female and multiple-carcass groups all significantly decreased time spent searching, whereas males in the female-and-carcass group did not alter time allocated to searching. Our results demonstrate that environmental cues do influence which alternative tactic male burying beetles use, and that the chosen tactic is influenced by the availability of both receptive females and carcasses on which to breed.

Alternative mating behaviours, prevalent across a wide range of taxa, are characterized by multiple distinct behavioural phenotypes of the sexually selected sex, typically males (Shuster, 2010; Waltz & Wolf, 1984). Most alternative reproductive behaviours comprise multiple tactics expressed in a condition-dependent manner (Dominey, 1984; Taborsky, Oliveira, & Brockmann, 2008). These conditional strategies are characterized by alternative phenotypes that are influenced by an environmental cue or some aspect of the male's condition or status (Gross, 1996; Lee, 2004; Shuster & Wade, 2003; Tomkins & Hazel, 2007). Conditional strategies occur when there is a certain threshold or switchpoint at which males switch from expressing one tactic to the other; this switchpoint could be an intrinsic quality of the individual, such as size, or an extrinsic environmental cue (Shuster & Wade, 2003; Tomkins & Hazel, 2007).

While some conditional strategies are characterized by an irreversible developmental switch, as documented in salmonid fishes (Aubin-Horth & Dodson, 2004; Piché, Hutchings, & Blanchard, 2008), many others exist in which shifts between tactics are rapid and reversible. This specific type of conditional strategy is termed a 'behavioural strategy' and is characterized by phenotypically plastic males that can switch between tactics based on an extrinsic cue, such as their relative status in the population (as in the status-dependent selection model of Gross, 1996), or another environmental cue, such as population density or resource availability (Brockmann, 2001; Shuster & Wade, 2003).

Such phenotypically plastic behavioural strategies are most likely to evolve when males have few mating opportunities, but when the availability of mating opportunities can be predicted by the environment (Shuster & Wade, 2003). In this case, males will perceive the environment as 'fine-grained', as it may change rapidly and multiple times throughout an individual's life (Brockmann,

* Correspondence and present address: S. K. Sakaluk, Behavior, Ecology, Evolution & Systematics Section, 4120 Biological Sciences, Illinois State University, Normal, IL 61720-4120, U.S.A.
E-mail address: skakal@ilstu.edu (S. K. Sakaluk).

http://dx.doi.org/10.1016/j.anbehav.2015.07.025
0003-3472/

2001; Levins, 1968; Shuster & Wade, 2003). In the context of male mating behaviours, the environmental grain may be determined by the spatiotemporal distribution of females (Shuster & Wade, 2003). Environments in which the circumstances surrounding a successful reproductive attempt are highly variable may also result in phenotypically plastic mating behaviours (Shuster & Wade, 2003).

Alternative tactics comprising behavioural strategies are known throughout diverse taxa. Commonly, the alternative phenotypes are expressed in response to the immediate environmental conditions, as when individuals adjust their tactic according to their status relative to competitors. However, instances may exist in which the current environment is not indicative of the reproductive landscape as a whole and provides little information on which tactic use is optimal. Such may be the case with alternative mate-finding tactics, where all males find themselves in a similar immediate environment devoid of reproductive resources at the time they have to decide which tactic to use. In this case, males may use information gained from past experiences with respect to the availability of reproductive resources in making their decision on which tactic to use.

Male *Nicrophorus* burying beetles represent an ideal model with which to test whether individuals use experience in decisions about tactic use. To successfully reproduce, burying beetles require a small vertebrate carcass, a rare and ephemeral resource. The two alternative mate-finding tactics used by male burying beetles are to actively fly in search of a carcass on which to meet a female and raise a brood, or to emit pheromone in the absence of a carcass (henceforth termed 'signalling'; Müller & Eggert, 1987). If a searching male is able to successfully locate a carcass, he may be presented with a number of different situations, depending on the presence of other beetles. If another male is already present, the two fight over possession of the resource (Müller, Eggert, & Dressel, 1990; Sakaluk & Müller, 2008). If a female is present on the carcass, the pair prepare and bury the carcass, mating repeatedly in the process. When no females are present on the carcass when the male arrives, he superficially buries the carcass and emits pheromone to aid in attracting a female (Eggert, 1992; Pukowski, 1933; Wilson & Fudge, 1984), which might inadvertently attract conspecific males or congeners of either sex that may attempt to usurp the resource (Eggert & Sakaluk, 2000; Haberer, Schmitt, Schreier, & Müller, 2011; Müller & Eggert, 1987). While this tactic is risky, it can have a high payoff; in *Nicrophorus vespilloides*, the average paternity on a single carcass for a successful searching male is likely to be 84%, with paternity up to 92% if there are no satellite males present (Eggert, 1992).

The signalling tactic is unlikely to have as great a return per brood, but probably has lower costs in terms of risky agonistic encounters and energetic demands. Females are attracted to the scent of the pheromone emitted by signalling males, and they cannot determine whether a male holds a carcass until they come into physical contact (Eggert & Müller, 1989a,1989b). Upon meeting a signalling male, the female allows a single copulation before flying away (Eggert & Müller, 1989b), probably to ensure an adequate supply of viable sperm in case she locates a carcass on which another male is not present (Eggert, 1992). Field studies have found that between 19 and 39% of females raise broods without a mate, presumably using sperm stored from mating with signalling males (Eggert, 1992; Müller, Braunisch, Hwang, & Eggert, 2007; Scott & Traniello, 1990). It is estimated that signalling males can achieve 5% paternity of a single clutch if they are the last male to mate with a female (Eggert, 1992). However, their actual success depends on how long it takes for a female to subsequently locate a carcass, how many additional males she mates with and whether another male is present on the carcass. It follows that a signalling male must mate with many females to achieve similar reproductive returns as a searcher. In spite of the difference between single-clutch paternities between the two tactics, a field study of *N. vespilloides* estimated that up to 45% of all larvae were sired by signalling males (Eggert, 1992; Müller et al., 2007).

All male burying beetles use both tactics, but the proportion of time spent using each tactic differs between individuals. While there is genetic variation underlying these behaviours, it does not account for all of the variation, and there is even substantial variation in behaviour within an individual (Eggert, 1992). Thus, these behavioural phenotypes are best viewed as alternative tactics within a conditional strategy. As a conditional strategy, there should be intrinsic or extrinsic cues that influence tactic expression. Previous studies have found that small males signal more frequently than large males, and that the influence of this intrinsic cue is not contingent on interactions with other beetles (Beeler, Rauter, & Moore, 1999; Walling, Stamper, Salisbury, & Moore, 2009). However, it is likely that there are also extrinsic environmental cues that influence a male's relative investment in the alternative tactics.

Because the reproductive success of male burying beetles is dependent on the spatiotemporal distribution of females and carcasses, experience with these resources may provide a valuable cue, allowing males to determine which tactic is likely to have greater returns in their specific environment. We tested this hypothesis by observing the behaviour of naïve male *Nicrophorus orbicollis* before and after exposure to different reproductive experiences. We predicted that if males are able to gain information about the distribution of resources from their experience, they should adjust the relative amount of time invested in each tactic accordingly. Specifically, males that are allowed to mate with multiple females in the absence of a carcass may perceive a greater availability of potential mates; we predicted that these males would increase investment in signalling and decrease investment in searching. Males that encounter multiple carcasses should perceive a greater abundance of carcasses, which may yield higher returns for searching. We predicted that males encountering carcasses would increase investment in searching and decrease investment in signalling. However, if a male encounters a carcass in nature but is unable to attract a female, the carcass is of no reproductive value. Thus, we exposed males to carcasses with or without females present to determine whether the presence of a female affects a male's perception of reproductive opportunities and differential investment in the alternative tactics.

METHODS

Experimental Animals

Nicrophorus orbicollis occurs throughout eastern North America, primarily inhabiting hardwood forests. Experimental individuals were second- and third-generation laboratory-reared descendants of beetles caught in baited pit-fall traps in autumn 2013 at the Parklands Nature Preserve near Lexington, Illinois, U.S.A. (40°39′57″N, 88°53′49″W). Field-caught individuals were brought into the laboratory and maintained in plastic deli containers (0.5-litre) with moist paper towels as a substrate, either individually or with another individual of the same sex. The beetles were fed small pieces of ground beef twice per week, at which time the paper towels were replaced with clean ones.

Field-caught beetles were paired randomly for breeding. Each pair was placed in a breeding chamber with a defrosted, previously frozen 20 g mouse carcass. When at least one member of the pair began inspecting the carcass, the beetles and the carcass were transferred to another container with moist peat. The pairs were then placed in a darkroom and allowed to mate, bury and prepare