Commentary

EVOLUTION OF COLONIALITY VIA COMMODITY SELECTION: WHAT ABOUT VARIANCE?

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How does coloniality evolve? The answer to that question remains elusive despite decades of research (Ward and Zahavi 1973, Siegel-Causey and Kharitonov 1990, Hoogland 1995, Brown and Brown 1996, Danchin et al. 1998, Rolland et al. 1998). Scientists traditionally approached coloniality from an economic framework (Ward and Zahavi 1973, Witttenberger and Hunt 1985, Richner and Heeb 1995, Brown and Brown 1996). This research program weighed potential costs and benefits in an attempt to uncover the overriding advantages that produce coloniality. Recently, Danchin and Wagner (1997) suggested an abandonment of the economic approach and proposed commodity selection as a better conceptual framework for the study of coloniality. With commodity selection, benefits are irrelevant for colony formation and the subsequent evolution of coloniality. This framework shifted the focus from benefits of coloniality to mechanisms responsible for coloniality.

Commodity selection, the synthesis of the hidden lek hypothesis and the performance-based conspecific attraction hypothesis, describes a behavior in which individuals select a commodity (e.g. habitat or mates) and, as a byproduct, aggregate at that location (Danchin and Wagner 1997, Wagner et al. 2000). For example, animals might prospect potential breeding habitats and choose to breed in favorable environments. Such a scenario could indirectly result in colonial breeding. Selecting suitable breeding habitat requires the use of some cue(s) that reflects fitness (and predicts future fitness) in a given environment. The proximate mechanism at the forefront of research on this topic involves the evaluation of conspecific reproductive success and is formulated in the performance-based conspecific attraction hypothesis (hereafter termed "habitat copying;" Wagner et al. 2000). The habitat copying hypothesis attempts not only to explain how coloniality evolved but how individuals make settlement decisions among colonies once established. Many empirical investigations of this hypothesis have appeared recently (Danchin et al. 1998, 2001; Erwin et al. 1998; Doligez et al. 1999, 2002; Schjorring et al. 1999; Brown et al. 2000; Serrano et al. 2001; Suryan and Irons 2001).

We agree with much of the commodity selection hypothesis and wish to improve upon this emerging approach to the study of the evolution of coloniality. Although commodity selection can produce coloniality as a byproduct, the proximate cues may not strictly involve average reproductive success (fitness surrogate) of potential breeding sites. A site's (i.e. a colony's) reproductive success comprises a distribution of individual reproductive output values. However, a distribution offers more information than simply the mean. The average reproductive success (μ) of a site represents the first moment of the distribution, whereas variability in reproductive success (σ) represents the second moment. To our knowledge, authors have not investigated variance of reproductive success as a potential cue reflecting fitness attributes of the local environment. Ecologists and evolutionary biologists should wonder why we exclude much of the information from the distribution when investigating the phenomenon

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of coloniality as well as other endeavors. In this commentary, we aim to demonstrate (1) the importance of variance in fitness as it relates to coloniality and (2) the likelihood that the proximate mechanism of commodity selection involves variability in reproductive success.

Mean versus variance.—Although much theoretical and empirical work has evaluated foraging patch assessment (e.g. Clark and Mangel 1984; Stephens 1987; Shettleworth et al. 1988; Valone 1989, 1993; Valone and Giraldeau 1993), similar studies investigating breeding patch selection only emerged recently (Switzer 1993, 1997; Forbes and Kaiser 1994; Boulinier and Danchin 1997; Schjorring 2002). Optimal foraging theorists have long recognized the importance of both mean and variance in fitness attributes (e.g. Caraco 1981, Clark and Mangel 1984, Caraco et al. 1995, Kacelnik and Bateson 1996); however, research into commodity selection has yet to include variance as an important parameter of study.

Commodity selection is a general hypothesis that states that individuals assess and select commodities (i.e. colonies); it does not specify particular cues used in the decision. With one exception, all tests of the habitat copying hypothesis have evaluated mean reproductive success of colonies as the cue for prospecting individuals (Danchin et al. 1998; Doligez et al. 1999, 2002; Brown et al. 2000; Serrano et al. 2001; Suryan and Irons 2001). The sole exception used a much coarser estimate of colony reproductive success (successful vs. unsuccessful colonies, Erwin et al. 1998). Reproductive success is measured in many ways but most authors report fledglings per nest or pair (only birds have been empirically investigated) (Kosciuch et al. 2001). Mean reproductive success is simply the arithmetic average of whatever measurement the authors designate as success for all individuals at a site (e.g. clutch size, nest success, body condition).

Environmental variability can substantially influence fitness on a global or regional scale (e.g. among colonies), as well as at a local scale (e.g. within a colony) (Brown and Brown 1996); thus, reproductive differences often exist within and among potential breeding sites. An ideal cue would accurately reflect all ecological and environmental effects on fitness (e.g. climate, food, predation) and honestly indicate individual fitness for the next breeding bout.

Studies that evaluate habitat copying assume that basing settlement decisions solely on the average reproductive success of a patch (PRS, an estimate of expected reproductive success in a patch) maximizes individual fitness; however, this may not be true. The evolutionary consequences reflected by variability in fitness components (e.g. variance of reproductive success) may prove to be as important as the consequences reflected by mean fitness. A complete cue would essentially pick up where the mean left off and additionally account for effects of variability. In fact, variance in reproductive success (or another fitness variance cue) in a breeding patch can often indicate overall fitness consequences more reliably than the mean.

To illustrate that point, consider two colonies of 10 organisms each (Fig. 1A). Colony A is composed of five individuals with zero fitness (e.g. number of offspring) and five individuals with a fitness of six (n = 30 total offspring). All individuals in colony B have a fitness of two (n = 20 total offspring). Although colony A has the higher average fitness, the two colonies also differ in fitness variance. Ideally, a behavioral strategy would evolve that perfectly optimizes fitness by choosing the breeding habitat (i.e. colony) with higher fitness opportunities. It turns out to maximize fitness an individual should choose to breed in the less variable colony where average fitness is lower. Below, we describe the reasons for this somewhat counterintuitive result.

For the purpose of our discussion, fitness will be defined as number of offspring in a trait-lineage (i.e. genotype or phenotype). Our goal is to compare the relative fitness of two alternative trait-lineages: one lineage that consistently chooses to breed in colony A, and the other in colony B. Thus, we assume that a given habitat cue (e.g. mean or variance in reproductive success) in year t accurately predicts conditions in year $t + 1$. We will track the fitness of a pair (because many colonial organisms are sexual species) over their lifetime. Let us assume for present purposes a breeding life of four years. To simplify computations while providing an intuitive understanding of the underlying principles, we also assume equal sex ratio, all offspring survive, and all pairs that we track produce equivalent numbers of offspring each year within a given colony. To estimate fitness, we monitor the growth of a trait-lineage by counting the accumulation of all offspring pairs
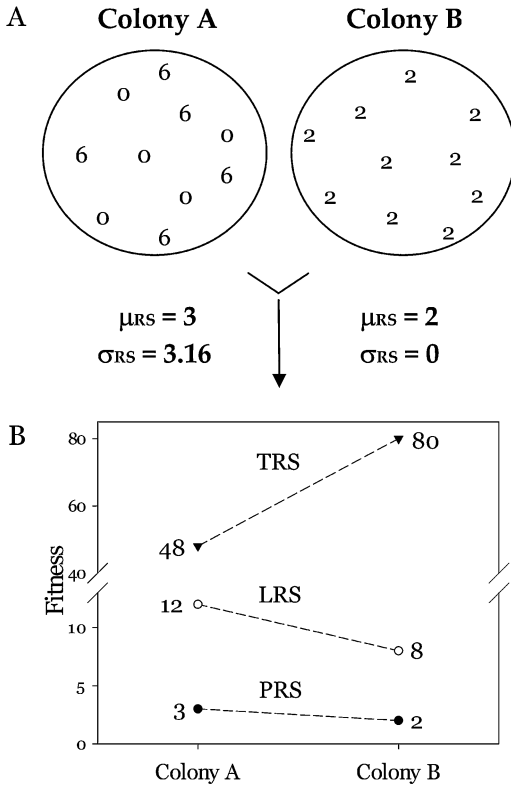
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a breeding pair that produces two offspring pairs per year (e.g. consistently choosing colony B) exhibits a TRS of 80 (i.e. total of 3 pair at end of year 1, 9 pair in year 2, 27 pair in year 3, 80 pair in year 4 after subtracting death of original pair). Although some authors suggest using the growth rate of a phenotype or genotype (e.g. malthusian parameter m_{ij}, multiplication rate λ) as a fitness estimate (e.g. Murray 1992, Danchin et al. 1995), we feel TRS is a more intuitive metric for illustrative purposes and clearly reflects the relative success of alternative lineages.

Let us now examine the relative success of a variable lineage (i.e. breeds in colony A each year) compared with an invariant lineage (i.e. breeds in colony B each year). Individuals of the variable lineage produce either zero or six offspring pairs per year with equal probability. Individuals of the invariant lineage produce two offspring pairs each year. Constructing a probabilistic model, we performed 1,000 iterations of this scenario. On average, the variable lineage grew at a faster rate—quadrupling in size per generation versus tripling in size for the invariant lineage—and exhibited higher patch average reproductive success (PRS) and lifetime reproductive success (LRS) than the invariant lineage (Fig. 1B). However, in 70.4% of the simulations, the invariant lineage surpassed the variable lineage in TRS (i.e. lineage size). We present median values of PRS, LRS, and TRS for each lineage (Fig. 1B). On average, the invariant lineage was 6.4× as large as the variable lineage, partly due to the fact that the variable lineage went extinct in 7% of the iterations, whereas the invariant lineage never went extinct. It is important to note that, because of the nature of branching processes, effects of variance amplify as lineages grow larger. For example, we performed 1,000 iterations of this scenario for a species that breeds for 10 years: the invariant lineage grew, on average, to a size >3,300× larger than the alternative trait-lineage. In this case, even if we ignore instances where the variable lineage went extinct, the invariant lineage was, on average, 147× as large as the variable lineage. Therefore, consistently selecting the least variable-breeding habitat, not necessarily the most productive on average, should increase overall productivity.

We recognize the difficulties in calculating LRS (Tella et al. 1998, Murray 2000) and assume TRS calculations for a colonial species are even

Fig. 1. (A) Fitness opportunities for two hypothetical colonies, with 10 individuals each, that differ in fitness mean and variance. Each number represents the number of offspring a pair produces in the colony. Most studies term this measurement of fitness "reproductive success." Variable μ_{RS} is mean reproductive success and σ_{RS} is the standard deviation. (B) Three alternative measures of fitness for a pair that selects to breed in either colony A or B throughout its four breeding years of life. Median values from 1,000 iterations of this scenario are presented. Patch average reproductive success (PRS) is the arithmetic mean success in a given colony. Lifetime reproductive success (LRS) represents the sum of all offspring pairs produced during the lifetime of a pair. Total reproductive success (TRS) is the sum of all offspring produced by the lineage of a pair during its lifetime (details in text). Numbers beside the symbols in the graph depict actual median values of fitness for the respective trait-lineage.

produced directly and indirectly by a breeding pair. We term that measurement total reproductive success (TRS), which represents the number of offspring in the lineage attributable to the original pair at the time of their death (offspring, grand-offspring, etc.). For instance,

more arduous. However, a direct measurement of that parameter is unnecessary. The standard deviation of reproductive success (σ_{RS}) is readily obtained in field studies and represents an excellent measurement that approximates the fitness consequences captured by TRS.

Variance as a cue.—Variability of fitness components (e.g. reproductive success) should be of great importance to colonial organisms because they persist in fluctuating environments (Wittneberger and Hunt 1985, Brown and Brown 1996). Sources of nest mortality often vary greatly (e.g. nest predators, ectoparasites, starvation) among breeding patches, resulting in differences in the mean and variance of reproductive success between sites. Further, colonial birds exploit patchy ephemeral resources, which helps create a situation where variance often abounds (within and among sites). Several of the cost–benefit hypotheses propose that coloniality evolved as a specific adaptation for increasing foraging efficiency (Brown and Brown 1996). By increasing the frequency of successful foraging bouts, an organism thereby reduces variability in success. That benefit is in accordance with that of optimal foraging theorists' investigations into benefits of social foraging.

In addition to foraging strategies, those organisms often exhibit reproductive strategies (e.g. brood reduction, underproduction of eggs) that maximize reproductive potential via variance reduction amid a fluctuating environment (Lack 1954, Boyce and Perrins 1987, DeWitt 1997, Monaghan and Nager 1997, Murphy 2000). Despite recognition of the importance of variance by students of the evolution of clutch size (e.g. optimization of geometric mean fitness), variability has not yet been considered a potential cue for prospecting individuals. However, if settlement decisions were based solely on the mean, individuals would run the risk of settling in highly variable colonies and suffering decreased productivity.

Because variance in reproductive success often abounds within and among colonies, it might serve as a figurative beacon of fitness potential. Variability within a colony might be easily assessed because prospecting individuals search at the local scale (Reed and Oring 1992, Reed et al. 1999) and some species are often observed searching individual nests (Boulinier et al. 1996). Furthermore, in certain cases (e.g. Fig. 1), choosing the appropriate breeding site

is imperative (i.e. drastic fitness differences); but the cue must involve variability rather than solely the average success to maximize fitness. In those circumstances, it is seemingly simple for an organism to assess variability in reproductive success (or environmental cues reflecting variability), whereas assessment of mean reproductive success appears more difficult. Selection should therefore favor a strategy that uses a "fitness invariance" cue to select a stable environment that maximizes overall reproductive output. Indeed, we might expect to find an integrated mean–variance cue in many situations because both parameters could convey important fitness information.

The question now becomes, How can this be tested empirically? We believe the answer is simple and in several cases, the data already exists and only awaits analyses. It merely requires that the measure of success in the study contain a measure of variance (e.g. not colony wide categories, such as successful vs. unsuccessful colonies; Erwin et al. 1998).

Most analyses previously evaluating mean reproductive success (μ_{RS}) can also be performed with the standard deviation of reproductive success (σ_{RS}). Some authors rank colonies by μ_{RS} and colony growth (Danchin et al. 1998, Brown et al. 2000) and plot the data to test for a correlation between highly productive colonies and colonies that attract the most individuals. That technique could easily be performed with σ_{RS} and comparisons between the two graphs (e.g. μ_{RS} vs. immigration and σ_{RS} vs. immigration) could then be evaluated. Although researchers can simply reiterate previous analyses, we propose a new procedure be conducted.

We suggest standardizing data (e.g. colony growth, μ_{RS}, σ_{RS}) by year to eliminate year effects while maintaining distribution information (e.g. magnitudes of differences among colonies). Because all assumptions of the habitat copying hypothesis apply for σ_{RS} as well, tests of differences among colonies and autocorrelation across time should also be performed with σ_{RS}. We also feel that the effects of μ_{RS} and σ_{RS} on colony choice (growth) should be tested simultaneously. An easy means of accomplishing this is to test the effects of μ_{RS} and σ_{RS} on colony growth using multiple regression (e.g. colony growth$_{(t)}$ = $\mu_{RS}'_{(t-1)}$ + $\sigma_{RS}'_{(t-1)}$ + $\mu_{RS}'_{(t-1)}$ × $\sigma_{RS}'_{(t-1)}$ + ε). Because the mean and variance of reproductive success might covary in certain cases, we also suggest

the evaluation of mean-variance correlations. Although a fitness invariance cue might not represent the holy grail in the study of the evolution of coloniality, it certainly might elucidate mechanisms partly responsible for coloniality in many cases. When critical attention is given to alternative cues potentially involved in the evolution of coloniality, such as σ_{RS}, finer resolution and a more robust understanding of this perplexing breeding system may be achieved.

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