

natural selection that dominate the latter half of a mutation's life. Much of this importance, however, depends on exactly how rare advantageous mutations are. If advantageous mutations are common, then the fate of any individual mutation is not important, eventually one of the mutants will make it to fixation. However, if advantageous mutations are rare or even unique, such as some gene duplications or rearrangements might be, then population-size fluctuations may be very important indeed. At present we know too little about how to spot an advantageous mutation to estimate its mutation rate, although looking at the rate of accumulation of new mutations under continued selection provides a good place to start¹².

Acknowledgements

I thank Norman Johnson for comments

and Sally Otto and Mike Whitlock for helpful discussions.

Patrick C. Phillips

Biology Dept, University of Texas at Arlington, Arlington, TX 76019-0498, USA
(pPhillips@uta.edu)

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Secondarily solitary: the evolutionary loss of social behavior

William T. Wcislo and Bryan N. Danforth

An understanding of the evolution of social behavior has been critical in formulating general evolutionary principles (e.g. kin selection¹). Often these studies are dominated by an *a priori* assumption that eusociality – social behavior involving a sterile caste of workers (Box 1) – is an evolutionary endpoint⁴. That is, eusocial ancestors give rise to descendant species that are also eusocial, unless they evolve social parasitism⁵. As applied to insect sociality, ‘Dollo’s law’ of irreversible evolution^{6,7} holds true for termites (Isoptera), ants (Formicidae), paper wasps (Vespidae), honeybees (Apini), stingless bees (Meliponini) and bumblebees (Bombini) – we know of no reversals to solitary nesting within these exclusively eusocial clades⁸⁻¹¹.

Wilson¹² hypothesized that these taxa irreversibly crossed a threshold of social integration. Among insects, the benefits of sociality (e.g. more-efficient work, improved defense) are enhanced by strict division of labor, but the resulting co-dependency may make it difficult to regain the full behavioral repertoire of solitary individuals^{12,13}. As a general rule, however, there are no *a priori* reasons to suggest that the evolution of eusociality must be irreversible. Eusociality, like any phenotypic trait, is not inherently ‘advanced’ relative to alternatives such as solitary behavior

Studies of social behavior frequently assume that evolution proceeds from a solitary state to a social one, and that social lineages give rise to lineages that are also social, excluding parasitic taxa. Recent phylogenetic studies of some bees contradict this assumption, and more examples are known or hypothesized in other animals. Social behavior can be lost to give rise to species that are secondarily solitary. Studies of the conditions that lead to the suppression or loss of social behavior can help to illuminate those factors that lead to its origins and maintenance.

William Wcislo is at the Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, USA (WcisloW@ic.si.edu); Bryan Danforth is at the Dept of Entomology, Cornell University, Ithaca, NY 14853, USA (bnd1@cornell.edu).

or communal nesting, and different environmental circumstances may favor one lifestyle over the other¹²⁻¹⁶.

The possibility that eusociality can revert to solitary behavior has been hypothesized previously¹²⁻¹⁴, especially by biologists studying halictine bees¹⁵⁻²⁰, yet reversals have been shown empirically only in recent years. Phylogenetic studies of taxa that contain both solitary and social species reveal evidence of apparent evolutionary transitions from eusocial to solitary behavior, contradicting the assumption of unidirectional social evolution. Here, we highlight recent studies and discuss their implications for our understanding of the evolution of social behavior (see also Refs 13, 14 and 20).

Phylogenetic methods and character mapping

Widespread use of cladistic methodology is generating a growing data base that facilitates hypothesis-testing of historical patterns and allows the inference of ancestral states²¹⁻²³. We will not discuss the strengths and weaknesses of different methodologies, except to note that reconstructing ancestral character states is dependent on the veracity of the phylogenies²⁴. Hypotheses that require the fewest number of *ad hoc* assumptions about evolutionary changes in character states are preferred over

Box 1. Social terminology

Social behavior is a composite phenotypic trait that has been defined in a variety of ways, and its definition is contentious²³. To avoid confusion, we explicitly define terms only for purposes of this review. Descriptive terms are properly applied to individuals or societies, although sometimes they are used at the species level to facilitate communication and analyses³.

Solitary behavior: each female occupies her own nest without any other adults and is solely responsible for rearing her brood.

Social behavior: group-living by more than one adult in which the dominant-subordinant relationships among the individuals (if any) are unspecified.

Eusocial behavior: sociality characterized by the presence of adults of more than one generation, among which there is a division of labor and some individuals are effectively sterile.

Communal behavior: social groups of more than one female in which each adult is reproductively active and there is minimal or no cooperation among nest-mates.

Subsocial behavior: parental behavior in which the adult(s) feed and guard the immature offspring until the latter are adults.

hypotheses that require more assumptions, in the absence of biological information that justifies a more-complex explanation²⁷.

Evolutionary changes in character states can be reconstructed from phylogenetic information as follows²³. First, a cladogram is generated using available data for the taxa of interest. There is no unanimity on whether a character of interest (e.g. sociality) should be included in the data set used to construct a cladogram, or whether it should be excluded²⁶. Then, beginning at the tips of the cladogram and working toward the base, character states are mapped onto the cladogram in a way that minimizes the number of changes needed to explain the phyletic distribution of character states (Box 2).

Evolutionary reversions to solitary behavior

Bees in the family Halictidae and Apidae are distantly related²⁷. Accumulating evidence from these taxa challenges the views that eusocial behavior is an evolutionary endpoint, and that social evolution is unidirectional. In some lineages, social behavior is lost or suppressed, apparently giving rise to solitary species from eusocial ancestors. Each study reviewed below is based on cladistic methodology; data used to reconstruct the historical relationships among species were independent of social behavior, and the behaviors were mapped onto cladograms at the end.

Halictine bees

The tribe Halictini (Halictidae) includes 26 genera of small to moderately sized solitary, social and parasitic bees distributed throughout the world¹⁶ (also C.D. Michener, pers. commun.). Two genera in particular, *Halictus* and *Lasioglossum*, are excellent taxa for studies of social evolution; each contains numerous species that differ in behavior, and each provides examples of the loss or suppression of social behavior. Representative life cycles of temperate, solitary and social halictine bees are given in Box 3.

Packer¹⁷ analyzed the phylogenetic relationships among eight species of *Lasioglossum* subgenus *Evyllaenus* using 26 informative allozyme loci. Based on a cladogram for species with known social behavior, Packer hypothesized that eusociality is the ancestral state. Among the species analyzed, there may be at least one, and possibly two, reversals to solitary behavior. Depending on the relationships among subgenus *Evyllaenus* and other subgenera of *Lasioglossum*, *L. (E.) fulvicorne* may either represent a reversal to solitary behavior or indicate that solitary behavior is the ancestral state. A

re-analysis of these data, including five additional species, supported the original conclusion²⁰.

Again using allozyme data, Richards¹⁸ analyzed the phylogenetic relationships among 15 species of *Halictus*, which represented a broad taxonomic sampling of the genus. She obtained 45 equally parsimonious trees that were summarized by two alternative consensus trees. These trees support the hypothesis that all species of *Halictus* considered in the analysis share a social ancestor (or one that facultatively expressed social or solitary behavior), and that eusociality may have reverted to solitary behavior in at least two lineages (or, solitary behavior is fixed in those populations studied). A re-analysis of a modified data set supported the original conclusion²⁰.

Augochlorine bees

The tribe Augochlorini (Halictidae) includes more than 30 genera of bees, most of which are brightly colored and neotropical¹⁹. At least three genera, *Augochlora*, *Augochlorella* and *Pereiraps*, contain eusocial species. In an analysis of 81 morphological characters, Daniorth and Eickwort¹⁹ obtained three phylogenetic trees following successive approximations character weighting. This analysis indicated that eusociality arose in the common ancestor of the eusocial taxa, but reverted to solitary behavior in one derived taxon, the subgenus *Augochlora sensu stricto*. Reversal to solitary nesting in this subgenus co-occurs with a switch from ground nesting to wood nesting²⁸, which may influence rates of parasitism and hence benefits associated with group-living²⁹.

Australian allodapine bees

Allodapine bees form a monophyletic tribe within the family Apidae (*sensu Ref. 30*). Allodapines are most abundant in sub-saharan Africa and Australia but also occur in other areas of Old World tropical and austral regions. Some form of weakly social behavior is present in almost all allodapine genera (except *Halterapis*³¹ and parasitic species). In comparison with most other social bees, the social behavior in allodapines is unusual. Females build nests in dry, pithy plant stems and offspring are not reared in individual cells like most bees. Instead, immatures live together in a common burrow where they have extensive contact with adult females.

Three genera of allodapines occur in Australia: *Braunsapis*, *Exoneura* and *Inquilina*. Reyes and Schwarz³² inferred phylogenetic relationships among the subgenera and species of the Australian genus *Exoneura* using a data set comprised of 43 morphological characters and 173 variable nucleotide sites from DNA sequences of two mitochondrial genes. Analyzing the combined data (a total of 216 characters), they obtained one tree in which the subgenus *Exoneurella* was found to be the sister group to subgenus *Brevineura* + *Exoneura sensu stricto*, and resolved the species-level relationships in *Exoneurella* as follows: *E. tridentata* + [*E. lawsoni* + (*E. setosa* - *E. eremophila*)], *E. tridentata*, members of the subgenus *Brevineura*, and all other (non-parasitic) Australian allodapine genera are eusocial, suggesting that the ancestral condition for the genus *Exoneura* is eusociality. That *E. setosa* and *E. eremophila* are solitary was most parsimoniously interpreted by Reyes and Schwarz³² as a reversal to solitary behavior in the common ancestor of these two species.

Loss of social behavior in other taxa

The belief that evolutionary processes are irreversible is so widespread it is canonized as 'Dollo's law', although there are exceptions to this so-called law^{6,7}. Thus, the notion persists that the evolution of sociality is always or usually

Box 2. Parsimony analyses applied to identifying reversals in social behavior

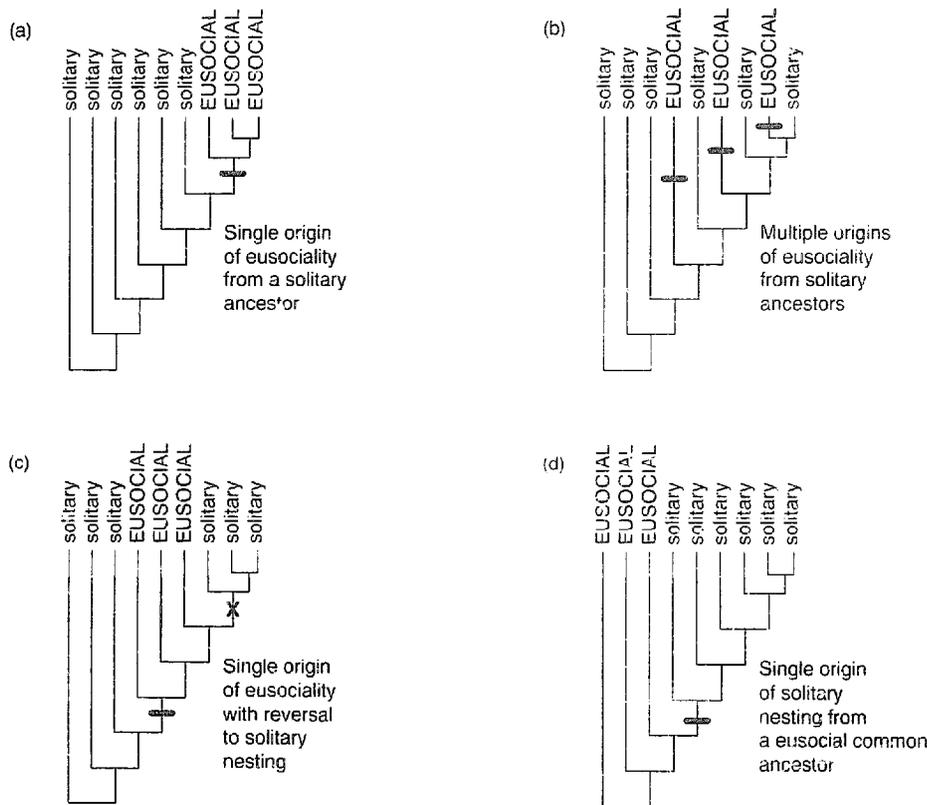
Imagine a group of nine species, three of which are eusocial and six solitary. For nine taxa with a phylogenetic root, there are 2027 025 fully resolved, bifurcating trees. In (a-d) we consider four of these alternative topologies and the implications of each for inferring the history of social evolution. In cladogram (a), the eusocial species form a monophyletic group that has descended from a solitary ancestor; eusociality is a terminal state. This hypothesis represents the unidirectional view of eusocial evolution: solitary living is ancestral, eusociality is derived, and there are no reversals to solitary behavior.

In (b) the eusocial taxa are each separated by solitary sister taxa or, more precisely, separated by primitively solitary sister clades. According to this cladogram eusociality is again derived relative to solitary living, but eusociality in each of the three taxa is not homologous. Intrinsic and extrinsic factors could have selected for the behavior independently, producing a pattern of parallel evolution.

According to (c), eusociality has arisen once, but descendants of the eusocial taxa have reverted to solitary living. Cladograms of this type directly contradict the unidirectional view that eusociality is always derived relative to solitary behavior. Observed reversals of this kind could shed light on what factors might favor solitary living in groups which are ancestrally eusocial.

Finally, in (d) we present an alternative in which eusociality appears to be ancestral to the nine in-group taxa, with solitary life evolving later. Investigations of additional taxa (other out-groups) might reveal that eusociality has arisen even earlier than indicated by this cladogram.

These hypothetical cladograms and reconstructions of ancestral character states illustrate the important point that we make no *a priori* assumptions about the direction of evolutionary change. As a null hypothesis, a gain or a loss of a trait is equally likely to occur. In other words, we do not weight one kind of change over the other. Some hypotheses of relationships (e.g. c and d) are best interpreted as reversals from eusociality to solitary nesting, but others (e.g. a and b) imply the opposite polarity.



unidirectional³³. Reversals to solitary behavior are not restricted to bees, but have been documented or hypothesized to occur in diverse invertebrates and birds (Table 1; also Ref. 14). An overly strong emphasis on the origins of eusociality means that we may be neglecting a widespread and important evolutionary transition: solitary behavior arising from common ancestors with social behavior.

Evolutionary reversions or condition-sensitive phenotypes?

The studies reviewed above apparently document evolutionary reversions (i.e. the loss of a capability to express a trait). These studies, however, have not eliminated the al-

ternative hypothesis that the observed behavior (character state) is the result of a developmental system that facultatively expresses different phenotypes under different conditions, without evolutionary change. This alternative hypothesis is plausible because, as shown in the following section, several thoroughly studied species show high levels of intraspecific variation in social behavior within and among populations.

The dearth of behavioral information for many social insects creates a potential pitfall in applying phylogenetic methods to comparative studies³. The behavior of most halictid species, for example, is unknown, or is based on information derived from a small number of individuals from one or a few localities^{16,19}. The phylogenetic approach can encourage typological thinking by forcing us to make the assumption that character states observed in one population (or one nest²⁰) are representative of the species, or one species is representative of the genus, etc., which may or may not be justified³.

If a social trait is absent in one population (or species) and present in related populations (or species), it does not necessarily imply an evolutionary loss in the first population. Rather, some organizing feature of the environment that is used as a developmental cue may be absent from that population, with the result that the trait is never expressed. For example, in montane populations of a bee (*Exoneura bicolor*) females frequently join kin to co-found nests, although the

trait does not occur in natural heathland populations of the same species⁴¹. Hurst *et al.*⁴² show that these behavioral differences arise as a consequence of the physical distribution of nesting substrates. By mimicking the montane distribution of nesting substrata in heathland, the level of kin co-founding increases to montane levels.

Intraspecific variation in social behavior as an analytical tool

Recent studies of various species show that nests of solitary and social individuals co-occur within a single population¹⁶. In two species of facultatively social carpenter bees (*Xylocopa*, Apidae), for example, Stark⁴³ and Hogendoorn

and Velthuis⁴⁴ showed that social behavior is favored during some periods, and solitary behavior during others. Variability in social organization may be maintained by natural selection in response to temporally varying environmental conditions (e.g. fluctuating parasite levels, nest site or pollen availability). Expression of different phenotypes may result from allelic differences among individuals or from individual condition-sensitive developmental systems that produce different phenotypes under different environmental conditions⁴⁵.

Geographical patterns of intraspecific variation in social behavior can be used as a tool to ascertain which environmental features facilitate the loss or suppression of social behavior. Egg-to-adult developmental times, adult longevity and the duration of the growing season interact to create a 'window of opportunity' for mother-daughter interactions and, by extension, for the evolutionary maintenance of matrilineal social groups, if group-living is beneficial.

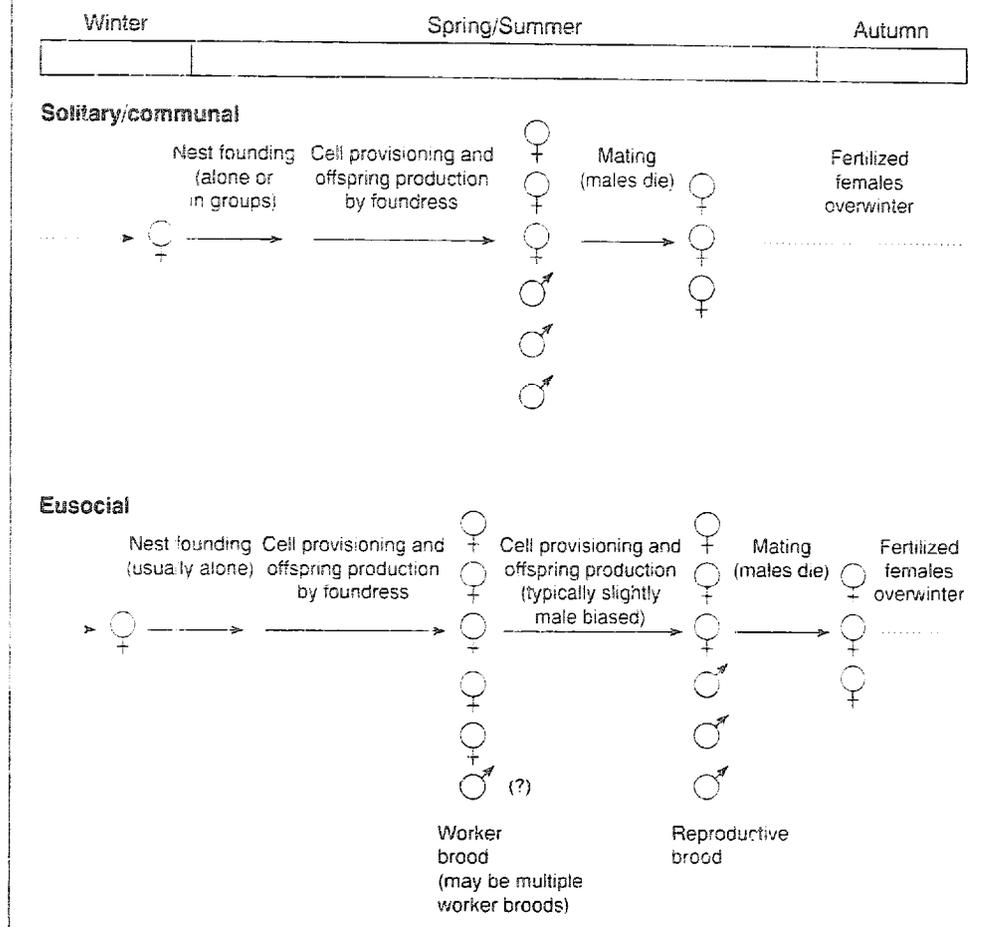
Mother-daughter interactions are possible only when two conditions are met. First, an overlap of generations requires that either the egg-to-adult developmental time is sufficiently brief so that mothers are still living when their daughters emerge as adults or adults are sufficiently long-lived. For example, the developmental time of a largely solitary *Lasioglossum (Dialictus) figueresi* is almost 80 days, and most mothers have already died when the brood emerges, effectively precluding mother-daughter interactions⁴⁶. Secondly, eusocial colonies by definition have at least one brood comprised mostly of worker females, prior to the production of the reproductives. Thus, generation time must be sufficiently short, and the period of foraging activity sufficiently long, so that at least two broods can be produced within the growing season at a locality (Box 3).

A variety of studies at high latitudes and high altitudes in temperate regions suggest that there is a tendency to shorten or eliminate the matrilineal stage at the colder limits of their distributions. For example, the Holarctic sweat bee *Halictus rubicundus* is distributed across Eurasia and northern North America, where it extends to the southern United States⁴⁷. Its nesting biology has been studied briefly at vari-

Box 3. Life cycle of a temperate eusocial sweat bee

There is considerable variation in the life cycles of social halictid bees. Caste is typically determined during adulthood. A generalized life cycle of a temperate species has roughly three phases. (1) Solitary foundress phase: a nest is excavated in the spring by a foundress female that produces a small number of offspring, most of which are female, constituting the first brood. (2) Inactive phase: after provisioning a number of cells, the solitary foundress ceases foraging and remains within the nest, waiting for the first-brood offspring to emerge as adults. (3) Matrilineal phase: a large percentage of the first-brood females remain within the natal nest as workers for their mother; some percentage of the first brood females may immediately enter diapause and return as foundresses the following spring. If the mother dies, then a worker becomes the replacement queen. Worker females provision cells with pollen and nectar, on which the queen lays eggs. During the matrilineal phase, bees produce one or more broods depending on the duration of the growing period and the developmental time of immatures. In temperate regions the number of worker broods varies with the length of the summer. The sex ratio in the worker brood(s) is typically female-biased, but becomes more balanced in the reproductive brood(s). At the end of the growing season, newly emerged females and males mate; eventually the males die, and mated females diapause during the unfavorable season to begin the cycle the following year.

Intraspecific variability exists in the percentage of nests that develop social behavior or remain solitary. Within social nests, variability exists in the following: the degree of size dimorphism between workers and queens (if any); the sex ratio of the first brood; the number of 'worker' broods; the proportion of workers that mate; the proportion of workers that have developed ovaries and are reproductively active; and the colony size.



ous lower-elevation sites in Europe and North America, and one New York (USA) population has been intensively studied. At these localities most bees live in social nests.

At a high-elevation site in the western United States (2850 m) female *H. rubicundus* begin foraging for pollen and nectar in mid-June, when flowers begin blooming⁴⁸. Females forage for pollen in late June and early July and then cease activity. In late July and August, newly eclosed male and female offspring emerge and mate; males die, and females overwinter to establish new nests the following year. At this site, the growing season is too short to permit two generations of the developmental rate of *H. rubicundus*; consequently, all females are solitary nesters.

A similar pattern is known in a transpalaeartic sweat bee, *Lasioglossum (Eurylaeus) calceatum*, which occurs

Table 1. Loss of social behavior in taxa other than bees

Group	Trait that is lost or suppressed	Number of events	Phylogenetic information?	Refs
Thrips (<i>Oncothrips</i> , <i>Kladothrips</i>)	Soldier caste	1-2? ^a	Yes	14
Aphids (Hormaphididae and Pemphigidae)	Soldier caste?	0-1? ^b	Yes	34
Cockroaches (Polyphaginae)	Gregarious behavior ^c	2 ^d	Yes	35
Cockroaches (Zetoborinae + Blaberinae + Gyninae + Diplopterinae)	Gregarious behavior	4 ^e	Yes	35
Spiders (<i>Stegodyphus</i>)	Colonial living	1 ^f	No ^g	36
Australian treecreeper (<i>Climactris</i>)	Cooperative breeding	1	No	37
Wren (<i>Campylorhynchus</i>)	Cooperative breeding	1	No	37
Scrub jays (<i>Cyanocitta</i>)	Cooperative breeding	1	Yes	37
Scrub jays (<i>Aphelocoma</i>)	Cooperative breeding	1?	Yes? ^h	37,38
Ascidians (<i>Enterogona</i> , <i>Pleurogona</i>)	Coloniality?	0-1?	Yes	40

^aAn alternative phylogenetic hypothesis that cannot be rejected unequivocally suggests that a soldier caste has not been lost.

^bThe phylogenetic analysis supports either four origins and one loss of a soldier caste or five origins.

^cAn aggregation of nymphs that eventually includes some adults.

^dThe two putative losses occur in lineages that are scored as polyphenic, so gregarious behavior may be suppressed rather than lost.

^eOne putative loss occurs in a lineage that is scored as polyphenic, so gregarious behavior may be suppressed rather than lost.

^fSocial spiders live in communal webs, and this study found approximately 25% of the spiders were solitary; it is unknown whether the solitary behavior represented an ontogenetic stage or was a fixed trait for those individuals.

^gBased on intraspecific comparisons.

^hThe phylogenetic hypothesis has been criticized by Brown and Li⁴².

ⁱA phylogeny for eight species from different genera shows that the loss of coloniality requires one more character state change than the origin of coloniality from solitary ancestors.

throughout Siberia, Europe and North Africa, to east and central Asia, including Japan⁴⁹. At lower elevations, the social organization is typical of a eusocial halictine bee (Box 3). At a high-elevation site in Japan (1167 m), however, female *L. (E.) caiceatum* are solitary, again presumably due to the shortened growing season.

In temperate regions there are parallels in phenological patterns between increasing altitude and latitude⁵. Examples of solitary behavior by individuals in areas at their latitudinal extremes strengthen the interpretation that the duration of the growing season sets an upper limit to the number of generations that can be produced, thereby influencing the expression of social organization. For example, *Augochlorella striata* is a widespread halictine bee in the eastern half of North America, from Florida as far north as Cape Breton Island, Canada (~45°N). Throughout most of its range, a colony produces two or more broods, and females live in eusocial groups; however, at the limit of its northern range, most nests are solitary⁵⁰.

Schwarz and co-workers^{41,51} have been studying intraspecific variation in social behavior in allodapine bees. They studied various populations of *Exoneura bicolor* and *E. richardsoni* along a latitudinal gradient from a cool temperate region in southern Australia (Victoria) to a sub-tropical region in the north (New South Wales). In contrast with halictine bees^{16,47,48}, *Exoneura* show limited variation in their number of generations under different climatic conditions⁵¹. Correspondingly, the potential for mother-daughter social groups is limited; nevertheless, there is considerable variation in the expression of social behavior.

The breadths of reaction norms for social phenotypes can apparently vary considerably, at least for some species, although there are scant data^{14,16}. The development of social phenotypes in species like *Halictus rubicundus*, for example, is weakly canalized and permits the expression of solitary behavior in areas where seasonal constraints preclude social behavior. In contrast, *H. ligatus* is unable to live in areas where seasonal constraints permit only a single generation,

perhaps because of an inability to express solitary behavior⁵².

Implications for studies of social behavior

Extant solitary taxa are frequently used as models to study factors that might contribute to the origins of sociality. But the existence of secondarily solitary taxa complicates such studies. For example, social insects can discriminate between nest-mates and non-nest-mates, which is important for maintaining the cohesiveness of social groups⁵³. Hölldobler and Michener⁵⁴ hypothesized that kin discrimination may have its evolutionary origin in an ability by solitary females to recognize individual nests using olfactory cues. A recent study showed that solitary *Lasioglossum (Dialictus) figueresi* female bees can discriminate be-

tween their own and alien nests on the basis of chemical cues⁵⁵. This study could be interpreted as support for the Hölldobler-Michener hypothesis that solitary behavior is ancestral for this species; alternatively, if solitary behavior is derived, then the ability is atavistic and hence not relevant to questions on the origins of sociality.

Conclusions

The studies outlined above show that phylogenetic information provides an empirical basis to formulate specific hypotheses of character state transitions, which can alter conclusions drawn from comparative data. In the absence of a phylogenetic framework, statements of character state change are untested assertions that depend on *a priori* assumptions about how evolution 'should' proceed. Biologists have historically tended to view sociality as advanced relative to solitary nesting. Several studies now document the reverse pattern within independent clades of predominantly social bees, showing that, in at least some cases, our *a priori* assumptions have no empirical basis. Eusocial behavior, like any other complex phenotypic trait, is presumably expensive to maintain because of costs such as an increased likelihood of disease and parasite transmission⁵⁶. Thus, in the absence of compensating benefits, there are reasons to predict that eusociality would be lost or suppressed under appropriate ecological circumstances. The evolutionary loss of social behavior opens a new window through which we can observe sociality from a different perspective. An understanding of how behavioral and environmental factors interact to create conditions favorable to the loss of social behavior should provide new insights into how and why social behavior evolves, and what environmental factors contribute to its origins and maintenance.

Acknowledgements

We are grateful to Bernie Crespi, Adam Cronin, Raghavendra Gadagkar, Laurence Packer, John Pandolfi, Stephen Reyes and Mike Schwarz for information or

manuscripts in press. For helpful comments on the manuscript we thank M. Schwarz, B. Crespi, A. Cronin, Nick Bull, Katja Hogendoorn, Don Windsor and an anonymous reviewer. W.T.W. received support from general research funds of the Smithsonian Tropical Research Institute, and B.N.D. received support from a USA National Science Foundation Research Grant in Systematic Biology (DEB-9508647).

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Plant functional classifications: from general groups to specific groups based on response to disturbance

The history of research in community ecology has often been compared to a pendulum oscillating between holistic, generalizing, and reductionist, specific views. From that perspective, the renewed interest in classifying species into groups that relate directly to function through shared biological characteristics, rather than phylogeny, is not surprising. Recently published approaches involving the analysis of sets of biological attributes fall into four main types of functional classifications of plant species. In order of increasing specificity of objective, these are: (1) emergent groups – groups of species that reflect natural correlations of biological attributes; (2) strategies – species within a strategy have similar attributes interpreted as adaptations to particular patterns of resource use; (3) functional types – species with similar roles in ecosystem processes by responding in similar ways to multiple environmental factors; and (4) specific response groups – contain species which respond in similar ways to specific environmental factors. The two latter categories, however, represent substantial recent conceptual advances stimulated by research aimed at predicting the effects of global change on vegetation dynamics^{1,2}. The goals are twofold: to build models that simulate shifts of vegetation types with changing climate³; and to provide land managers with models that can be used in a variety of situations, including cases where detailed

**S. Lavorel, S. McIntyre,
J. Landsberg and
T.D.A. Forbes**

Predicting the effects of anthropogenic changes in climate, atmospheric composition and land use on vegetation patterns has been a central concern of recent ecological research. This aim has revived the search for classification schemes that can be used to group plant species according to their response to specified environmental factors. One way forward is to adopt a hierarchical classification, where different sets of traits are examined depending on growth form. Also, at the level of interpretation, the environmental context and purpose of functional classifications need to be specified explicitly, so that global generalizations can be made by comparing across environments functional classifications derived from similar methodologies.

S. Lavorel is at the Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, UPR 9056, 34293 Montpellier Cedex 5, France; S. McIntyre is at the CSIRO Division of Tropical Agriculture, 306 Carmody Rd, St Lucia, QLD 4067, Australia; J. Landsberg is at the CSIRO Division of Wildlife and Ecology, PO Box 84, Lyneham, ACT 2602, Australia; T.D.A. Forbes is at the Texas A&M University, Agricultural Research and Extension Center, 1619 Garner Field Road, Uvalde, TX 78801-6205, USA.

information is limited. More specifically, recognition of land use change as one of the main drivers of global change has raised the need to identify specific groups based on disturbance response. This activity builds on knowledge acquired from the development of the more general classifications (1–3 above).

Emergent groups – classifications based on correlations of biological attributes

Emergent groups reflect the combination of adaptive responses and of evolutionary constraints appearing as sets of correlated traits. They are identified in an inductive manner, using multivariate analyses of usually large sets of traits – covering life history, morphology, physiology, phenology and regeneration biology – expected to determine species behaviour in the ecosystem. Such classifications tend to not address any ecosystem function explicitly or, when they attempt to, lack relationship to particular mechanisms¹. They tend to produce sets of traits essentially corresponding to main life forms (trees, shrubs, grasses and forbs), although the degree of detailed subdivision depends on the breadth of the spectrum taken from global^{4,5}, to regional^{6,7} and to a particular vegetation type^{8–10}. Yet classifications into emergent groups have been useful to identify broad correlation patterns, such as relationships between plant size or seed mass and