Corrections

CELL BIOLOGY. For the article “The NF1 tumor suppressor critically regulates TSC2 and mTOR,” by Cory M. Johannessen, Elizabeth E. Reczek, Marianne F. James, Hilde Brems, Eric Legius, and Karen Cichowski, which appeared in issue 24, June 14, 2005, of Proc. Natl. Acad. Sci. USA (102, 8573–8578; first published June 3, 2005; 10.1073/pnas.0503224102), the authors note the following. On page 8574, the last sentence of the first paragraph in the left column, “Clarified lysates were normalized for protein levels and analyzed by Western blotting with the following antibodies: phospho-p70S6K (T-389), phospho-tuberin (S-939), phospho-tuberin (T-1462), phospho-Akt (S-473), tuberin (C-20) from Santa Cruz Biotechnology, and protein kinase Bo/AKT1, actin, and β-tubulin from Sigma-Aldrich,” should read: “Clarified lysates were normalized for protein levels and analyzed by Western blotting with the following antibodies: phospho-p70S6K (T-389), phospho-tuberin (S-939), phospho-tuberin (T-1462), phospho-Akt (S-473) from Cell Signaling Technologies, tuberin (C-20) from Santa Cruz Biotechnology, and protein kinase Bo/AKT1, actin, and β-tubulin from Sigma-Aldrich.” On page 8574, the second sentence of the second paragraph in the left column, “For lentiviral production, HEK293T cells were transfected with the Δ8.2 lentiviral construct (encoding gag, pol, rev), VSVG, and either empty pKO vector or the pKO vector containing the following sequence transcribing short-hairpin RNAs specific to NF1: 5’-TTATAAATAGCCTGGAAAAGG-3’,” should read: “For lentiviral production, HEK293T cells were transfected with the Δ8.2 lentiviral construct (encoding gag, pol, rev), VSVG, and either empty pKO.1puro vector or the pKO.1puro vector containing the following sequence transcribing short-hairpin RNAs specific to NF1: 5’-TTATAAATAGCCTGGAAAAGG-3’.” In addition, the authors would like to add the following statement to the Acknowledgments: “We would also like to thank Dr. William C. Hahn (Harvard Medical School and Dana–Farber Cancer Institute, Boston) and the Broad Institute (Cambridge, MA) for the pKO.1 lentiviral constructs.”

BIOCHEMISTRY. For the article “Engineered single-chain dimeric streptavidins with an unexpected strong preference for biotin-4-fluorescein,” by Filiz M. Aslan, Yong Yu, Scott C. Mohr, and Charles R. Cantor, which appeared in issue 24, June 14, 2005, of Proc. Natl. Acad. Sci. USA (102, 8507–8512; first published June 6, 2005; 10.1073/pnas.0503112102), the footnotes appeared in the wrong order, due to a printer’s error. The ** footnote on page 8507 should have read: “Throughout this paper, we use the terms monomer(ic), dimer(ic), and tetramer(ic) to refer to the number of biotin-binding domains present in a molecule, regardless of the number of polypeptide chains it has.” In addition, the †† footnote on page 8512 should have read: “We note, however, that extremely high-affinity mutants might not be recovered in this procedure due to near-irreversible binding of biotin from the culture medium.”

PERSPECTIVE. For the article “Eusociality: Origin and consequences,” by Edward O. Wilson and Bert Hölldobler, which appeared in issue 38, September 20, 2005, of Proc. Natl. Acad. Sci. USA (102, 13367–13371; first published September 12, 2005; 10.1073/pnas.0505858102), the authors note that Donat Agosti was omitted from the list of editors in ref. 48. The corrected reference appears below.

ANTHROPOLOGY. For the article “Descent of the larynx in chimpanzee infants,” by Takeshi Nishimura, Akichika Mikami, Juri Suzuki, and Tetsuro Matuzawa, which appeared in issue 12, June 10, 2003, of Proc. Natl. Acad. Sci. USA (100, 6930–6933; first published May 29, 2003; 10.1073/pnas.1231107100), the authors note that the symbols for Cleo and Pal were switched in the legend for Fig. 2. The figure and its corrected legend appear below. These errors do not alter the conclusions of the article.

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Fig. 2. SVT growth in the three chimpanzee infants: Ayumu (male, ●), Cleo (female, ■), and Pal (female, ▲). (a) Growth of the oral (solid line) and oropharyngeal (dotted line) components of the SVT↓. (b) Growth of the SVT↓ (solid line) and SVT↑ (dotted line). (c) Age-related changes in the ratio of SVT↓ to SVT↑ lengths.
Eusociality: Origin and consequences

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Contributed by Edward O. Wilson, July 12, 2005

In this new assessment of the empirical evidence, an alternative to the standard model is proposed: group selection is the strong binding force in eusocial evolution; individual selection, the strong dissolutive force; and kin selection (narrowly defined), either a weak binding or weak dissolutive force, according to circumstance. Close kinship may be more a consequence of eusociality than a factor promoting its origin. A point of no return to the solitary state exists, as a rule when workers become anatomically differenti-

ated. Eusociality has been rare in evolution, evidently due to the scarcity of environmental pressures adequate to tip the balance among countervailing forces in favor of group selection. Eusociality in ants and termites in the irreversible stage is the key to their ecological dominance and has (at least in ants) shaped some features of internal phylogeny. Their colonies are consistently superior to solitary and preeusocial competitors, due to the altruistic behavior among nestmates and their ability to organize coordinated action by pheromonal communication.

In eusociality, an evolutionarily advanced level of colonial existence, adult colonial members belong to two or more overlapping generations, care cooperatively for the young, and are divided into reproductive and nonreproductive (or at least less-reproductive) castes. The phenomenon is well marked and nearly confined to insects, especially ants, bees, wasps, and ter-
mites, where it has been subject to a large body of mostly specialized research scattered across disciplines from genetics to paleontology. It has long been the conviction of researchers on social insects that common principles exist at the organismic and superorganismic levels, thus between individual insects and the tightly integrated colonies they compose (1, 2). Parallels have been persuasively drawn between the self-construction of organisms from molecules and tissues and that of superorganisms from interacting entire organisms (3). The principles can be further parsed into two segments of the time scale: the developmental decision rules that assemble organisms and colonies in each generation and the origin of these rules through evolutionary time.

Focusing here on the second principle, evolutionary process, we suggest how three seemingly disparate evolutionary phenomena can be causally linked: the selection forces that generate and shape eusociality, the narrowness of the origin of eusociality, and the ecological hegemony of eusocial insects.

The Forces of Natural Selection

Research during the past half century has incrementally clarified the nature of the collective forces that create and shape eusociality. At the most basic level, an allele or ensemble of alleles prescribing phenotypic plasticity that includes self sacrifice of some members of groups will spread if the positive intra-
tergroup component of the altruists’ fit-
tesses exceeds the negative within-group component of the altruists’ fitnesses (4–6). Altruism is defined as behavior that benefits others at the cost of the lifetime production of offspring by the altruist. The forces that determine this outcome are group selection, the differential survival and reproduction of en-
tire cooperative groups as a result of the frequency of the eusociality alleles in each; individual direct selection, accruing from the differential personal survival and reproduction of each of the colony members; and kin (indirect) selection, which we define here in the original narrow sense as the favoring or disfavoring by individuals of collateral relatives, i.e., relatives other than per-
sonal offspring. The inclusive fitness of the prescribing genotype, of individual colony members and hence statistically the colonies they compose, is the nonad-

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tions (12). It promotes harmony among group members and genetic fitness of the group as a whole, once colony level is attained, and its effect is thereby inherently binding. Individual direct selection and kin selection play out in the social interactions of the colony members. By pitting individual members and nepotisms against one another, individual direct selection tends to reduce colony harmony and genetic fitness. Depending on circumstance, kin selection can be either binding or dissolutive, the latter by competition among nepotistic subgroups. In all of this multilevel theater of evolution, the gene remains the unit of selection, whereas the target of selection can be the individual, the group, or nepotistic alliances or otherwise biased actions within the group.

The Point of No Return

An abundance of evidence suggests that the strength of the biasing role of relatedness within a species depends on the stage of its social evolution. The key transition occurs at a point in colony evolution that can be conveniently called the point of no return (13). Beyond this level, it is impossible, or at least difficult and uncommon, for a species to regress from the eusocial to a more primitively eusocial, presocial, or solitary condition.

When in evolution does eusociality become irreversible? We infer that this comes very early in the evolution of that condition, in particular when an anatomically distinct worker caste first appears, hence when a colony can most meaningfully be called a superorganism. Three lines of solitary halictine bees and one of allodapine apid bees are known exceptions to this rule are several lines of polistine wasps and vespine wasp species that possess an evolutionary stage and circumstance, but it does not join group selection from environmental pressure in driving the system. Close genetic relatedness arises from eusociality but is not a necessary precondition.

In the second model, alleles exist that induce cooperation and possess phenotypic plasticity, which includes a nongenetic worker caste. If these alleles are favored by sufficiently powerful colony selection, eusociality can originate when founding members of the primitive colonies have low relatedness or, in theory (and albeit unlikely), none at all (18, 19). What counts is the common possession of eusociality alleles, not relatedness. However, the probability that others share such alleles is obviously higher in closely related than in unrelated individuals (after all, when such an allele arises, it most likely spreads in a population of relatives).

Thus, if the second, opposing hypothesis is correct, the high relatedness generally observed in even the evolutionarily primitive colonies could be a consequence than a cause of eusociality and not a necessity for its origin. Preeusocial groups formed of parents and offspring would automatically have close kinship. In the hypothe-

The Origin of Eusociality

A key question remaining is whether, in fact, relatedness is an important biasing factor and hence kin selection an important force in the origin and maintenance of eusociality. For the origin of eusociality before the point of no return, a new and alternative model should be considered. The two competing hypotheses can be compared as follows (see also Fig. 1).

Model A. In the standard model, altruism originates by selection of its prescribing alleles through a kin network. Kin selection is thus strongly binding, whereas individual direct selection is dissolutive. Group selection from environmental pressure and kin selection drive the system. Close genetic relatedness precedes the origin of eusociality.

Model B. In the alternative model, which we propose here, altruism originates by group selection of prescribing alleles whose phenotypic expression is flexible, directing individuals to become reproductive or workers according to physiological or behavioral cues. Kin selection can be absent, weakly binding, or weakly dissolutive, according to evolutionary stage and circumstance, but it does not join group selection from environmental pressure in driving the system. Close genetic relatedness arises from eusociality but is not a necessary precondition.
primitively eusocial wasps of the genus *Pheidole* demonstrate that relatedness plays a significant role in eusocial organization (24).

Evidence from living presocial and primitively eusocial species that might distinguish between the two hypotheses and shed light on the importance of genetic relatedness is still tenuous. But it is at least consistent with the second hypothesis, namely that relatedness is less powerful a factor and kin selection often more dissolutive in the early stages of colonial evolution than previously suspected. Xylocopine carpenter bees, which are facultatively semisocial and possibly examples of an early stage in the origin of eusociality, often form pairs, which then divide into queen and worker roles by means of a dominance order. Subordinates prefer to stay if unrelated but to leave if related. The result is consistent with kin selection but the effect is dissolutive rather than binding (20). Thus, group selection appears not to be yet strong enough to counteract dissolutive kin selection. Groups of bees in the alldapine genus *Exoneura* have higher per capita productivity when the members are closely related but individual reproduction approaches uniformity, as expected from group selection, and, if sustained in the absence of sufficiently strong colony selection, would seem to preclude the origin of an altruistic worker caste (21). In the very primitively eusocial wasp *Eustenogaster fraterna*, founding females have lower relatedness than sisters and, due to high adult turnover, the relatedness of unmated females to female brood is far lower ($r = 0.210 \pm 0.171$, 95% confidence intervals) (22). Among somewhat primitively eusocial paper wasps (Polistes), females act less aggressively toward genetic relatives than toward nonrelatives but do not favor close over distant relatives when founding colonies (23). Similar results obtained from the primitively eusocial wasps of the genus *Ropalidia* demonstrate that relatedness plays no significant role in eusocial organization (24).

In the later stages of eusocial evolution, past the point of no return, the favoring of close collateral kin has been depicted as dissolutive in some respects but also, and much more importantly (with some writers desiring to variable degree), as a strong binding force crucial to the maintenance of altruism and eusociality. A growing body of evidence of several kinds now suggests otherwise. It includes the rarity of male production by workers in colonies of social hymenopterans (ants, bees, and wasps), with one single-mated queen, contrary to the prediction from models of narrow kin selection (25); the lack of favoring bias by workers of their respective mothers in colonies with multiple queens, also at variance with traditional expectation (26, 27); and the existence of unexpected low degrees of relationship, in some cases approaching background values, in many species of ants (27). Moreover, nestmate recognition in the social Hymenoptera is by colony scent, which turns out to be a complex gestalt of hydrocarbons absorbed into the outer cuticle of the exoskeleton, shared by food exchange and grooming, learned by imprinting, and largely independent of kinship in composition (25, 28). In an ant checked for such correlations (*Pogonomyrmex occidentalis*), colonies with low relatedness among the workers have overwhelmingly higher growth and reproduction rates than those with high worker relatedness (29). This effect, favoring group selection as opposed to kin selection as the binding force, may be due to improved genetic resistance to disease or to the enhancement of division of labor by genetic proneness to specialization by the workers.

At the same time, a great many studies have implicated kin selection as a weak dissolutive force arising from nepotism and conflict among colony members. Its principal documented effect is the perturbation of sex investment ratios in the social Hymenoptera away from the expected 1:1 Fisherian balance. The perturbation stems from the haplodiploid mode of sex determination in the Hymenoptera, which causes ratios in singly mated mother queens (1:1) to differ from those of her daughter workers (more investment in new virgin queens than in males) (4, 5).

A second phenomenon possibly biased by relatedness and established in the later, irreversible stage of eusocial evolution is policing, the use of harassment or selective egg removal to restrict reproduction to the reproductive individual. Kin selection has been strongly indicated as a binding force in one species of social wasps, where policing decreases with the relatedness of the workers (30). On the other hand, the role of kin selection has been eliminated altogether in favor of group selection in the Cape race of the honey bee (31) and several species of ponerine and formicine ants (32–36).

The Rarity of Eusociality

The colonial insects thus seemingly command us to turn back to the external environment and group selection and away from a preoccupation with abstract models of kin selection if we are to best understand the origin and maintenance of eusociality. That frame shift is consistent with a remarkable phenomenon that has been in plain sight but largely overlooked by investigators: the phylogenetic rarity of eusociality. Of the \(\sim 2,600\) living taxonomic families of insects and other arthropods currently recognized, only 15 are known to contain eusocial species (13, 24, 37). Because six of the eusocial families are termites, the living species of which apparently derived from a single phylad, whereas eusociality of halictid bees originated in three independent events (15), the total number of known origins of eusociality in arthropods is 12.

It follows that some property of nature has set a very high bar for the attainment of eusociality. The inhibiting property is most likely to be the dissolutive force of individual direct selection. Even the large number of phyletic lines where individuals nest in aggregates and disperse to a limited degree, including those that reproduce by cloning ($r = 1$), have not in the vast majority of cases vaulted the bar. It seems to follow that
only some additional extraordinary circumstance or set of circumstances in their prior history and in the environmental challenge they faced lifted them over the bar. When those rare conditions exist, it is not difficult to imagine how the plasticity of a single genome can be molded by group selection first to create cooperative breeding and then caste systems (the defining property of eusociality). The adaptive programming of phenotypic plasticity to fit environmental contingency is a well-established principle of genetics (38). So even if colony selection renders some individuals sterile drudges or suicidal defenders, it does not matter, because neither deviants who leave to try their luck as solitary nor colonies weakened by their deviancy can compete against well-integrated colonies of the same species. Even if workers retain the ability to reproduce and dissipate individual selection remains potentially strong, their prudent cooperation could be enhanced by programming into the hereditary social repertory through the acceptance of “bribes” of small amounts of reproduction bestowed by the dominant queens or by the dominant collectivity of nestmates, or else the prospect of assuming the role of primary reproductive in the event of the death of the queen (39).

**Colony Selection as the Driver**

The defining nature of the programs of developmental plasticity in insect superorganisms can be more clearly visualized by the metaphor of the colony as a factory inside a fortress. The factory is the egg-laying queen together with the nurse workers who rear the young to maturity, whereas the fortress is the nest and the workers who build, repair, and guard it (12, 40).

Several evolutionary rules have emerged from decades-long studies of the insect fortress and factory. All point to ecological colony selection as the strong binding force of eusocial evolution. First is the necessity of preadaptation. The known eusocial phyletic lines with primitive species still living stand out among closely related solitary phyletic lines in adaptations that evidently predisposed them to forming colonies. In the Hymenoptera, for example, at least seven independent lines among the 60,000 or so known species of wasps and bees (with ants added, composing the division Aculeata of the hymenopteran suborder Apocrita) have evolved eusociality, evidently from ancestral species that built nests and fed their larvae with prey or pollen. In contrast, not one of the >70,000 known sawflies (suborder Symphyta) and parasitic hymenopterans (division Parasitica of the Apocrita) are eusocial, and in none extant do adults build nests or provision their young. Other eusocial species, those outside the Hymenoptera, have descended from species adapted to unusually well-protected microhabitats that can be most effectively used and defended by groups. They include green-wood borings (the ambrosia beetle *Austroplatypus*) (41), plant gallers (aphids and thrips) (42, 43), and, in the one known example among crustaceans, cavities in sponges (*Synalpheus* snapping shrimps) (44).

A second rule is consistent with the first: the key adaptation that led to eusociality is defense against enemies, specifically predators, parasites, and competitors (9, 45). Numerous studies, especially those on ants, have shown that groups are more effective in defense than solitary individuals and large groups more effective than small groups. In more advanced species, with larger mature colonies and recruitment communication, colonies gain further advantage from their superior foraging methods (25, 46).

Along with the establishment of the fortress has been the evolutionary development of the factory. The division of labor has grown stronger along phyletic lines, first between reproductives and workers and then within the worker caste. Communication has grown in complexity. Judging by comparison among living species, signals of fertility status and colony recognition were first; then alarm signals; next, recruitment to food sources and new nest sites by successful foragers; then mass foraging and, depending on the timing and spatial distribution of resources, long-lasting trunk trails; and finally, territorial defense by territorial pheromone marking, ritualized tournaments, and other sophisticated exchanges (25).

Correlative studies across large numbers of eusocial insect species provide strong evidence that the colony life cycle of each species, along with the details of its caste and communication system, has been shaped by the particular environments in which the species occurred through evolutionary time. The most important predictor of evolved social complexity is mature colony size (25, 46). Among species of eusocial bees and wasps, for example, an evolutionary increase in the populations was generally accompanied by elaboration of the division of labor, together with increased complexity in the modes of caste determination and changes in the modes of fertility signaling. Caste shifted from a flexibly behavioral relationship among anatomically similar females to complete dimorphism in which the status of colony members is determined in larval life or even in part genetically (13, 37).

Among the >11,000 known species of ants, mature colony size, varying by six orders of magnitude, is correlated with sociobiological trends parallel to those of bees and wasps. It is also manifestly adapted to nest sites and food habits particular to each species in turn. At one extreme are the tens of workers of some predatory ponerine colonies that occupy preformed cavities in decaying vegetation and specialize variously on polychrid millipedes, centipedes, beetles, and other restricted prey. At the other extreme are the gigantic colonies of African driver ants, with >20 million workers, that live in large excavated soil cavities and hunt in armies for a wide range of arthropod and small vertebrate prey (25).

The origin of colonies with mature colony populations of 106 and higher, bolstered by major innovations in colony organization, is a rare event, like the origin of eusociality itself. The weaving of arboreal nests from larval silk has originated in ants only three times worldwide. Army-ant behavior, marked by mass foraging, has appeared perhaps six times. Within this ensemble, swarm-raiding, in which the foraging army advances over a broad front, has appeared three times, in *Dorylus, Eciton*, and *Pheidole*, respectively. Fungus gardening has evolved only once in ants, in the New World attini, and within this tribe, it has advanced to the use of fresh foliage only once also, in the monophyletic leafcutter complex of *Acromyrmex* and *Atta* (25).

**Eusociality and Preemptive Ecological Success**

The breakthrough by two of the lines to eusociality has conferred on them spectacular ecological success. Although ants and termites together compose only 2% of the ∼900,000 insect species known globally, they make up more than half the insect biomass. Their dominance is ecological in origin. Colonies control nest sites and foraging grounds in competition with solitary insects. They use chemical communication to assemble nestmates and organized maneuverers to defeat adversaries. The disposition of workers to risk or surrender their lives enhances the genetic fitness of the mother colony. In general, ants in particular dominate the central, more stable areas of habitats, whereas solitary insects are best able to flourish in the peripheral, more ephemeral areas (25, 45).

How did this hegemony arise? The modern ant family (*Formicidae*) is dominated by four subfamilies, including the Ponerinae, a member of the anatomi-
...many lines) as granivores and collectors of homopteran sugary excreta. During the Eocene, the dietary versatility of the myrmicines promoted their advance into other habitats. The same expansion occurred even more disproportionately in the formicines and dolicichoderines, with a large number of species spreading both upward into the tropical forest canopies, which they now dominate in good part as cryptic herbivores on enriched sap transmitted as excrement by homopterans (49), and outward into temperate forests and xeric habitats around the world. By the mid-Eocene, ants had become numerically dominant insects. The history of the ants thus appears to have started with ecological preemption based on eusociality in the late Cretaceous or early Paleogene and to have continued with subsequent dynastic expansions into environments beyond the tropical forest ground layer (47).

**Broader Implications**

In the ants and other social insects, we are thus privileged to see not only how complex societies have evolved independently of those of humans and in a different sensory modality (mostly chemosensory versus audiovisual) but also, with increasing clarity, the relations between levels of biological organization and the forces of natural selection that formed and shaped them. We have also begun to glimpse, albeit still dimly and in fragments, connections between major features of the sociobiology, ecology, and biogeography of these insects.

If the conclusions drawn here about eusociality in insects and other arthropods are correct, they could have implications for advanced social behavior outside the arthropods. Rarity and the preeminence of group selection in unusual environments that favor cooperation are shared by the bathyergid rodents, the only highly eusocial phylum known in the vertebrates. Rarity of occurrence and unusual preadaptations characterized the early species of Homo and were followed in a similar manner during the advancement of the ants and termites by the spectacular ecological success and preemptive exclusion of competing forms by Homo sapiens.

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