

daytime [6,18] when melatonin is undetectable.

Preliminary studies measuring light-induced changes in EEG correlates of arousal have shown that blue light (460 nm) is more effective than green light (555 nm) at suppressing delta/theta activity (0.5–5 Hz), which is considered a marker of both the circadian and homeostatic drive for arousal. Furthermore, blue light preferentially activates high-alpha frequency oscillations (9.5–10.5 Hz) [5], which closely parallel the circadian rhythm of melatonin production [19]. It may be possible that different arousal responses have differing spectral sensitivities to light, theoretically mediated through differing relative contributions of the short-wavelength sensitive melanopsin-driven system and the longer-wavelength sensitive photopic and scotopic visual photoreceptor systems. Action spectra for the alerting effects of light on multiple EEG frequencies during both day-time and night-time exposures would address this question, and if combined with the simultaneous creation of action spectra for fMRI responses, would create a very powerful technique to establish the photobiological and neurobiological pathways through which light alerts the brain. We, along with many who wish to use light as a fatigue countermeasure in clinical, military and occupational settings, await these results with great interest.

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DOI: 10.1016/j.cub.2006.08.039

Behavioural Ecology: Promiscuous Fathers Sire Young that Recognize True Family

Most theories of kin selection assume that animals are able to distinguish relatives from non-relatives. This is especially difficult in situations where mixed parentage precludes that relatedness is recognised by familiarity. Recent work shows that, within the same brood, young bluegill sunfish that are fathered by cuckolders – but not those sired by parental males – pick out their relatives using self-referent phenotype matching and not familiarity.

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The theory of kin selection revolutionised our understanding of animal sociality by demonstrating that an individual can gain genetic benefits by

helping both its own progeny and/or a non-descendent kin [1]. Accordingly, individuals can increase their inclusive fitness disproportionately, as by helping relatives they pass more copies of their own genes on to the next generation. But can individuals

Box 1

Social systems that introduce genetic unpredictability between familiar individuals and predict the evolution kin recognition based on self-referent phenotype matching. Modified from [8,10].

Extra-pair copulations and quasi parasitism

Broods of full- and half-siblings reared together.

Brood parasitism

Young of different relatedness reared together (from relatives, if parasites are kin, to non-relatives, if parasites are non-kin or heterospecifics).

Interbrood aggregation

Young from different parents reared together, either through cooperative breeding, adoption/kidnapping or brood amalgamation.

Spatial hotspots

Kin and non-kin from different broods and generations aggregating for sexual displays (leks) and mate choice.

recognise kin that they had not met before? A new study by Hain and Neff [2] in this issue of *Current Biology* demonstrates that young bluegill sunfish (*Lepomis macrochirus*) seek out the company of unfamiliar relatives using chemical cues, despite having grown up in an unpredictable mix of mostly non-kin and some kin of varying relatedness.

At the evolutionary level of analysis, kin selection theory predicts that cooperation among relatives has discernable evolutionary benefits [1]. However, kin selection theory does not provide a predictive framework of when and how individuals should recognise relatives [3]. Research into kin recognition systems, instead, has traditionally focused on understanding the rules and cues that govern the function and development of social affiliation. Konrad Lorenz's classic study [4] on filial imprinting is still an important motivation for recent studies on the development of social preferences, such as the establishment of social referents and extrapolation towards more general recognition templates for mate preferences of zebra finches (*Taeniopygia guttata*), published in *Current Biology* earlier this year [5]. Familiarity appears to be a reliable social recognition cue in many species, including birds with 'helpers at the nest' [6], where uncertainty about relatedness to parents and siblings is typically low [7]. But many social behaviours

occur among strangers, suggesting that there must be mechanisms to recognise kinship beyond familiarity.

In general, individuals can discriminate between relatives and non-relatives using two separate recognition mechanisms: direct recognition involves the discrimination of individuals based on phenotypic traits that reflect the underlying genetic similarity [8]. Familiarity is one such direct recognition mechanism, when it can be assumed that familiar individuals are kin; another direct recognition mechanism is phenotype matching, whereby individuals are categorized as kin according to how well their phenotypic traits match the traits of a memorized or genetically determined recognition template, such as those learned from parents [3]. Unlike familiarity, phenotype matching thus allows individuals to discriminate between kin and non-kin even without prior exposure: kin should reliably resemble the recognition template to a greater extent than non-kin.

By contrast, indirect kin recognition involves affiliation with a group of individuals based on location or timing [3,8]. For instance, during the parental feeding visits of eastern phoebes (*Sayornis phoebe*) to their young nestlings chicks are recognised as progeny based on their age (pre-fledging) and location (inside own nest) [9].

More recently, behavioural ecologists have begun to study the

ontogeny of recognition systems in unpredictable social contexts [10]. Consider, for instance, how a brood parasite, such as the brown-headed cowbird (*Molothrus ater*), can recognise its own species when its early social environment consists of only host parents and nestmates that belong to a completely different species [11]. Indirect recognition is not feasible for cowbirds, because typically only a single parasite chick grows up in the host nest. Familiarity with or phenotype matching of foster parents' and nestmates' traits would also misidentify conspecifics. Instead, as Hauber and colleagues [12] have shown, young cowbirds inspect their own traits and later associate with individuals who match these self-traits closely, even when the self-traits were experimentally manipulated. This recognition mechanism has been termed 'the armpit effect' by Richard Dawkins [13].

Theoretically, such self-referent phenotype matching may be evolutionarily advantageous in a wide range of contexts in which social cues are unreliable for inferring the genetic relatedness of familiar individuals (Box 1). In support of this prediction, self-referencing has been suggested to explain preferred association with relatives in lekking manakins (*Manacus manacus*) where siblings often hatch alone and are unlikely to interact until maturity, peacocks (*Pavo cristatus*), whose early social environment includes a mix of relatives and non-relatives, and golden hamsters (*Mesocricetus auratus*) that had been cross-fostered to unrelated mothers and littermates (reviewed in [8]). There is even evidence for self-referencing in plants during competition between vegetatively propagated rootlets from the same original individual [14]. In humans, self-referencing is likely to explain how women can discriminate between odour cues from men, with whom they do or do not share specific alleles of the MHC-system [15]. Self-referencing has also been suggested to govern the paternal decision mechanisms to provide differential care in

nesting bluegill sunfish: parental males who have been cuckolded provide less attention to broods than males who sired their full brood [16].

Bluegill sunfish have gained scientific fame through their variable breeding system: females do not provide maternal care, instead the males build nests and protect and care for the offspring (Figure 1). During mating, females visit nest-holding males and release eggs [17]. In addition to these sex-role reversed couples, some male bluegills have developed yet a different mating strategy: cuckolders steal reproductive success from nest-building males by fertilising eggs after release by the female [17]. Consequently, cuckolders invest more heavily into sperm production and avoid the costs of nestbuilding and paternal care. A consequence of this reproductive strategy is that most broods will be derived from different fathers. As nest-building males also have multiple female partners, the relatedness of a brood of bluegill sunfish in a given nest is highly variable.

Only recently have questions about interaction between kin uncertainty and the mechanisms of social recognition systems been described in the context of mate choice, paternal care and kin discrimination [18]. In particular, genetic analyses revealed that parental blue-gill males and their multiple female partners sire most young in the nest, creating cohorts of full- and half-sibs, while the progeny of any cuckolder are surrounded by mostly unrelated individuals as well as some half and full sibs [2]. As such, one nest hosts a veritable cocktail of genotypes from several males and females which means that finding your relatives is not an easy task. Still, the effort may have important pay-offs because interactions with kin can lead to increased efficiency in foraging and more rapid growth rates [2].

In a series of carefully detailed choice tests Hain and Neff [2] demonstrate that the progeny of cuckolder males show consistent spatial preferences for chemical cues from unfamiliar relatives

Figure 1. Bluegill sunfish (*Lepomis macrochirus*).

A male bluegill sunfish showing characteristic male features. Some males of this species, however, mimic females and fertilise eggs that a female releases into the nest built by another male. Bluegill sunfish fry show spatial preference for waterborne cues of unfamiliar relatives, but only those that are sired by a cuckolder. Photo from Lake Opinicon by B. Neff.



compared to unfamiliar non-relatives. The source of these phenotypic cues and the sensory systems of progeny involved in perceiving the cues are yet to be uncovered. Nonetheless, the progeny of cuckolder males show a consistent behavioural association with kin, even when they had been reared in a mixed-paternity brood of one cuckolder and one parental male. These kin-directed behaviours of the progeny of cuckolder males are in contrast with those of the progeny of parental males, which do not show preferences for association with kin in the same choice tests.

Although the lack of behavioural discrimination does not imply lack of recognition or perceptual discrimination [19], the observed behavioural differences between parental and cuckolder offspring under the same experimental conditions clearly imply that different decision rules govern the affiliations of these fish. Offspring of neither type of male show discrimination between familiar and unfamiliar kin, indicating that generally familiarity plays no major role in kin discrimination in the bluegill. While this work follows other recent work on self-referent phenotype matching as an important mechanism for kin recognition [8], the authors take advantage of the external fertilization of bluegills and use *in vitro* methods to be the first to remove the possibility of *in utero* learning or indirect recognition between broodmates.

Using microsatellite data on relatedness of brood mates in natural nests, the authors are also

able to quantify the evolutionary benefits of kin discrimination in bluegill sunfish: by using self-referencing — rather than familiarity — to associate with kin, the progeny of promiscuous males may increase their fitness by a factor of four. Although ecologists had considered the diversity of the social contexts in which self-referencing may occur (Box 1), a further insight derived from this new work is that different cognitive decision rules are being used within one species, depending on the reproductive strategy of the father. What remains to be uncovered is whether the genomic and ecological control mechanisms that are involved in determining male breeding strategies are also involved in shaping the cognitive architecture of the progeny of males from either reproductive tactic.

As is the case for many complex social systems, such as that of the bluegill sunfish, familiarity alone will not solve the problem of discerning kin from non-kin. Broods of mixed paternity appear to be the rule and not the exception [20] and while there is mounting evidence that mating decisions are based on genomic recognition, we lack a basic understanding of the mechanisms that underlie these associations. We thus await experimentation on the role of self-referent phenotype matching not only in the context of cooperation among siblings, where related individuals are predicted to be present, but also within the ecology of optimal outbreeding through mate choice, and in the contexts of social transactions at large.

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DOI: 10.1016/j.cub.2006.08.036

Microtubule Mechanics: A Little Flexibility Goes a Long Way

Microtubules are the least flexible of the cytoskeletal filaments, yet they are occasionally seen to be severely buckled in cells. A recent analysis suggests these buckles are evidence of high contractile forces throughout the cytoplasm, and that the other elements of the cytoskeleton laterally reinforce microtubules to help prevent their collapse.

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Cellular microtubules do not bend easily. Unlike actin microfilaments and intermediate filaments which fill the cytoplasm as entangled meshworks, microtubules often radiate from perinuclear regions to cell margins as individual rods. Flexural rigidity is important for microtubules to function as superhighways for molecule and organelle transport through the cytoplasm, and for their function as dynamic struts that push and pull on chromosomes from a distance during mitosis. The microtubule's flexural stiffness derives from its form: as a hollow tube, the microtubule follows the engineering design principle that structures designed to resist bending should distribute material away from their central axis [1].

Indeed, the microtubule's resistance to bending is 100 times greater than that of the more compact actin filament, despite the fact that the actin and tubulin subunits are mechanically similar materials [2]. With both microtubule structure and function implying flexural stiffness, it is curious that microtubules can occasionally be found in highly bent configurations inside of cells [3].

In a recent study, Brangwynne *et al.* [3] investigated the mechanical implications of microtubule curvatures observed in living cells. Because thermal forces alone are too small to impart significant curvature to microtubules, an arching microtubule contour implies that it is being deformed by transverse loads or has buckled from

compression. From classical structural analysis of column buckling [4], it is expected that microtubules will buckle under piconewton compressive loads generated by polymerization and depolymerization [5], but the characteristic length of the waveform should be tens of microns long. While this analysis can account for the appearance of slowly arching microtubules connecting polarized centrioles to chromosomes aligned at the equator of a mitotic spindle, Brangwynne *et al.* [3] noted that microtubules in the cytoplasm of interphase cells often have highly localized bends with wavelengths of only a few microns. Using fluorescently labeled tubulin, the group documented short wavelength buckling of microtubules under three different conditions: first, when growing microtubules collided with the plasma membrane; second, when peripheral microtubules were actively compressed by deforming the plasma membrane with a microneedle; and third, when cells executed myosin-based contractions.

The observations of Brangwynne *et al.* [3] raise two questions: First, why does this form of buckling