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What we don't know, and what needs to be known, about the cooperatively breeding Acorn Woodpecker *Melanerpes formicivorus*

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Abstract. The Acorn Woodpecker *Melanerpes formicivorus* is one of a small number of woodpecker species that are cooperative breeders, living in family groups of up to 15 individuals of both sexes and all ages and exhibiting a complex mating system involving multiple cobreeders of both sexes (polygynandry). Although much has been learned concerning the social organisation and ecology of this species, over 45 years of research at Hastings Reservation, central coastal California, USA, has left us with a large number of unanswered questions ranging from relatively minor issues such as why adults have white eyes and why juveniles have a plumage similar to adult males to more major issues such as how cavity limitation could act as a driver of their unique social behaviours and how brood reduction is adaptive. Here we briefly discuss some of these questions and speculate as to how they might be addressed by future work. Long-term studies are important as a means of addressing many demographic and behavioural questions, but are even more valuable as a means of generating new questions that would have been overlooked without detailed knowledge of natural history and general ecology.

Key words: Acorn Woodpeckers, *Melanerpes*, caching behaviour, cooperative breeding, eye colour, food storage, juvenile plumage, social behaviour, cavity

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INTRODUCTION

Cooperative breeding, whereby some individuals help raise young that are not their own (Koenig & Dickinson 2004), is found in an estimated 9% of birds worldwide (Cockburn 2006) and is widely distributed taxonomically (Arnold & Owens 1999). Of the 182 species of true woodpeckers (subfamily Picinae) recognised by Winkler & Christie (2002), the proportion known or suspected to live in family groups and exhibit cooperative breeding is similar, with approximately 18 (9.8%) in this category. Of these, eight (44%) are members of the genus *Melanerpes*, a relatively large Neotropical genus of 22 species with eclectic and often diverse food habits, only rarely including the classical woodpecker habit of excavating for wood-boring larvae.

With over a third of species in this genus exhibiting cooperative breeding, *Melanerpes* exhibits far more sociality than any other major woodpecker genus and, although a critical phylogenetic analysis has yet to be performed, would appear to contain significantly more cooperative breeders than expected, similar to several genera of passerine birds including *Campylorynchus* wrens, *Malurus* fairy-wrens, *Pomatostomus* babblers, and *Cyanocorax* jays (Edwards & Naeem 1993). Studies of at least one other social *Melanerpes* species — the colonial Hispaniolan Woodpecker *M. striatus* — is ongoing, but otherwise none of the other highly social species in this genus has been studied in detail, and cooperative breeding is known only anecdotally in several.

Here we emphasise not what is known about the cooperatively breeding Acorn Woodpecker — one of the most extensively studied of all species in the family (Mikusiński 2006) — but rather what we do *not* know about its ecology, behaviour, and evolution. This wealth of questions is striking because it follows 45 years of work and two long-term studies of this species, including our own ongoing study at Hastings Reservation in central coastal California, USA, started in 1968 by Michael and Barbara MacRoberts (1976), and that of Peter Stacey and his colleagues in Water Canyon, New Mexico, conducted between 1975 and 1984 (Stacey 1979a, b, Stacey & Ligon 1987).

A BRIEF SUMMARY OF ACORN WOODPECKER SOCIAL BEHAVIOUR

Acorn Woodpeckers live in permanently territorial, polygynandrous family groups that typically include three factions: a coalition of between one and six males that compete for matings within the group, a coalition of one to three females that lay eggs communally in the same nest cavity, and up to 10 helpers that are offspring of the breeders from prior nests (Koenig et al. 1995b). Group composition is highly variable, however. Of 1547 group-years of data at our study site in central coastal California between 1972 and 2012, 39% of group-years consisted of a simple pair of birds, while 45% contained at least two cobreeder males, 23% two joint-nesting females, and 58% at least one helper. Helpers are of both sexes, although a modest majority (57.4% of 1294 helper-years between 1972 and 2012) were males, in the same direction as the slight but significant sex bias of fledglings (Koenig et al. 2001). Geographic variation is also considerable, with groups in a population studied in southwestern New Mexico being significantly smaller than the California population and exhibiting very little if any joint-nesting (Koenig & Stacey 1990), and those in a third population in southeastern Arizona being almost entirely pairs and generally migratory (Stacey & Bock 1978).

Kinship is a critical feature of Acorn Woodpecker societies. Cobreeder male coalitions are almost always brothers, a father and his sons, or a mixture of the two, whereas joint-nesting females are sisters or a mother and daughter. Despite this pattern of close genetic relatedness within groups, incest is rare, and helpers do not breed in their natal group (Koenig et al. 1998, Haydock et al. 2001). Instead, reproductive vacancies created by the death of the breeders (either males or females) within a group are filled by a coalition of (former) helpers (related to each other but unrelated to birds in the group that has the vacancy) from elsewhere. Once a vacancy is filled, however, helpers of the sex opposite that of the vacancy are able to inherit and cobreed along with their same-sex parents. Thus incest avoidance, rather than reproductive competition, is the primary driver of reproductive roles within groups.

Reproductive vacancies are often vigorously contested in 'power struggles' among coalitions of same-sex helpers, events that provide unequivocal evidence that helping is 'making the best of a bad job' and that helpers fight for the opportunity to give up their helper status and become breeders in the population.

Until recently, we assumed that the primary feature of the biology of Acorn Woodpeckers limiting dispersal and the creation of new territories in this species was primarily related to their granaries — snags or trees in which birds drill small holes in which they store acorns from the oaks (genus *Quercus* and *Notholithocarpus*) with which they are closely associated (Koenig & Mumme 1987). Recently, however, we have tested this hypothesis experimentally and found that, although granaries are important, cavities excavated by the birds and suitable for nesting are even more limiting (E. Walters and W. Koenig, unpublished data).

Groups exhibit a considerable range of apparently highly cooperative behaviours, including communal acorn storage, granary defence, and nesting, along with equally impressive competitive behaviours in the form of mate-guarding by males (Mumme et al. 1983a) and egg-destruction by joint-nesting females (Mumme et al. 1983b, Koenig et al. 1995a). Helpers contribute to most group functions, but the fitness consequences of helpers differ significantly depending on the sex of the helper and the size of the acorn crop (see below).

The effects of the acorn crop are dramatic. In years of large acorn crops, the breeding season, which typically will have ended in June or July, will start again in August or September as acorns mature. Such autumn nests fledge young as late as early November (Koenig & Stahl 2007). After a winter hiatus, groups will then resume nesting the following spring and potentially have two successive nests. In contrast, in poor crop years, birds are forced to abandon their territories, only occasionally returning the following spring after spending the winter off the territory (Hannon et al. 1987).

The acorn crop has other, more subtle effects as well. In particular, the effect of male helpers, measured as the increase in offspring produced per nest attributable to each helper, changes with the size of the acorn crop, being highly positive in good acorn crop years and negative in poor years, opposite the expectation of the hypothesis that helpers are necessary, and thus more beneficial, when ecological conditions are poor (Koenig et al. 2011). In contrast, female helpers have a positive but statistically non-significant effect on offspring production that does not vary with the acorn crop.

Regardless of which sex of helper one considers, the indirect (kin-selected) fitness benefits helpers gain by increasing the reproductive success of their parents are small compared to the advantages of breeding, thus supporting the hypothesis that helping is an inferior option compared to breeding. In addition to these kin-selected benefits, however, there are several potential direct fitness advantages that helpers could be gaining by provisioning offspring. For example, they could be gaining experience that helps them as breeders later in life (the 'skills hypothesis') or be helping in order to keep breeders from forcing them out of the group (the 'pay-to-stay hypothesis'). We have, however, as yet failed to find evidence for any of these potential direct fitness benefits (Koenig & Walters 2011).

WHAT WE DO NOT KNOW

Questions that elude us, even after more than 45 years of continuous effort, fall into several categories. Those we focus on here are divided arbitrarily into questions specific to Acorn Woodpeckers and those that are more generally applicable to woodpeckers or cooperatively breeding species.

Issues largely restricted to Acorn Woodpeckers

Why do adults have white eyes?

Fledgling Acorn Woodpeckers have dark eyes that gradually fade to the white eye colour of adults by the time of the postjuvenal moult, 3 to 4 months after fledging (Spray & MacRoberts 1975; Fig. 1). Intriguingly, all four of the 22 species of *Melanerpes* that have light eyes are either cooperative breeders (*M. candidus*, *M. formicivorus*, and *M. cruentatus*) or colonial (*M. striatus*). In addition, the Ground Woodpecker *Geocolaptes olivaceus*, one of the few non-*Melanerpes* woodpecker species that is a cooperative breeder, has light eyes as both adults and juveniles. Although this overall pattern suggests a relationship between sociality and light eyes, no such relationship has been noted in other taxa and comparably light eyes are found in several species of *Dryocopus* and *Campephilus* woodpeckers, none of which is social.

Most work on iris colour in birds has been conducted in the context of reproductive isolation and hybridisation. There is, however, some research supporting an association between iris colour and feeding behaviour across taxa (Ficken et al. 1971, Worthy 1978, 1991) and a study focusing on passerine birds found geographic differences — most notably a relatively high frequency of brightly-pigmented iris colour in south African and Australian birds, regions where cooperative breeding is relatively common — along with various associations with plumage and life-history. The same study, however, found no support for the hypothesis that iris colour is associated with social behaviour (Craig & Hulley 2004). More recently, an experimental study by Davidson et al. (2014) provided evidence that the pale white iris colour of Jackdaws *Corvus monedula*, another highly social (but non-cooperative breeding) species, functions to deter conspecific competitors from approaching occupied nest sites. Whether iris colour in Acorn Woodpeckers serves a similar signaling function is unknown, but given the importance of cavities for roosting and nesting, this is a plausible hypothesis.

Why do juveniles have adult male plumage?

Fledgling Acorn Woodpeckers are distinguishable from adults by several characters, including eye colour, duller plumage colouration, and distinct tail spots, most of which are lost in or about the time of the postjuvenal moult (Spray & MacRoberts 1975). Juveniles are notably distinct from adults, however, in that they are monochromatic in plumage and both sexes have the crown pattern of adult males with no black band separating the red crown from the white forehead (Fig. 1). To further complicate the situation, in Colombia, juvenile *M. f. flavigula* have completely red crowns and napes, adult males have the crown plumage of adult females in other parts of this species' range, and adult females have no red on their crown whatsoever (Winkler et al. 1995). Thus, juveniles in *M. f. flavigula* are monochromatic, as in other races, but distinct from adults of both sexes.

What is the functional significance of these patterns? There is no comparative analysis of juvenile plumage patterns in woodpeckers, and thus we do not know how common or rare it is for juveniles of this group to resemble adult males rather than adult females. Possibly there is

Fig. 1. Two fledglings on the right (note dark eyes and male-like crown plumage) begging from an adult (with white eye on the left). Also note the granary limb pock-marked with storage holes used for storing acorns. Photo © by Marie Read.

a connection with dominance, since males are generally dominant over females within birds of the same (breeder or helper) status (Hannon et al. 1987). Why this would not apply to birds in Colombia is unknown. This character would be relatively easy to manipulate experimentally, however, and behavioural observations, although difficult, could potentially reveal the fitness consequences of juvenile plumage, at least at the intraspecific level.

What is the functional significance of runt eggs?

Runt eggs are unusually small eggs that are deficient in some way, usually because they contain no yolk, and thus do not hatch (Koenig 1980a). They are found in all avian taxa but are generally quite rare; among woodpeckers in general, for example, the mean frequency of runt eggs is approximately 0.5% (Koenig 1980b). In contrast, the incidence of runt eggs in Acorn Woodpeckers is nearly an order of magnitude greater, being 4.8% in museum collections and around 3% among eggs at our study site in central coastal California (Koenig 1980b). In groups with a single female breeder, runt eggs composed 2.3% of 1661 eggs (Koenig et al. 2009). Their frequency among groups with joint-nesting females is apparently much higher, but is difficult to quantify because a high proportion of them are destroyed: of 24 runt eggs noted during our study of egg destruction by joint-nesting females, 19 (79%) were destroyed prior to the onset of incubation (Koenig et al. 1995a). Thus, our estimates of the frequency of runt eggs is most likely an underestimate.

Runt eggs are particularly common in the nests of joint-nesting females and typically are laid immediately prior to the laying of a normal egg and clutch. The exact nature of the association between runt eggs and joint-nesting remains obscure, however. Koenig et al. (1995a) considered four hypotheses: (1) runt eggs are a synchronising signal indicating when and where a female will lay her eggs; (2) they provide a critical nutritional benefit to the female that destroys them; (3) they minimise the energetic losses due to egg destruction; and (4) the production of runt eggs increases the opportunity for the last-to-lay female to destroy a normal egg laid by a cobreeder. None of these hypotheses was strongly supported. Behavioural observations provide some support for the last of these hypotheses, however: in 5 of 17 nesting attempts (29%), a female that laid a runt egg destroyed both her own egg and a normal egg laid on the same day by her joint-nesting female, typically resulting in the first female laying one egg more in the completed clutch than the number of (normal) eggs in the clutch contributed by the second joint-nesting female.

These findings suggest that runt eggs may help bias egg ownership within a joint clutch in favour of the bird laying the abnormally small egg. Our attempt to estimate the fitness consequences of laying a runt egg, however, indicates that they are minimal. Thus, the functional basis for the uniquely high incidence of runt eggs in Acorn Woodpeckers remains unclear.

Why does reproductive success increase linearly with the acorn crop?

The size of a granary places an upper limit on the number of acorns that can be securely stored by a group of Acorn Woodpeckers. The bulk of nesting takes places in March to June, many months after acorns are stored in the fall. Consequently, one would expect there to be a clear threshold set by the number of acorns that can be stored, beyond which a larger acorn crop would have little or no effect on the reproductive performance of the population the subsequent spring.

Contrary to this expectation, reproductive success appears to increase linearly with the overall size of the acorn crop, with no indication of a threshold (Fig. 2). What circumvents the expected threshold? One possibility is that acorns remain on the trees longer when the crop is large, thus reducing the length of time birds are dependent on their stored acorns (Koenig et al. 2014). It seems likely, however, that the mechanism is more complex, and that birds somehow capitalise on larger acorn crops in ways other than through their storage facilities so as to better survive the winter and be in better condition when the spring breeding season begins.

Partial support for birds being in better condition following large acorn crops comes from the finding that the relationship between the acorn crop and winter fattening was significantly positive, at least for males (Koenig et al. 2005). The mechanism behind this effect is unknown, although food supplementation experiments offer an opportunity for testing alternative hypotheses.

Why do Acorn Woodpeckers hide copulations, and what is the function of pre-roost mounting?

Although there is a considerable literature on copulation frequency in birds (Birkhead et al. 1987, Møller & Birkhead 1992), there is little regarding birds that hide their mating activities. Acorn Woodpeckers are one such species: mounting — both of females by males and vice-versa — is observed just prior to roosting in the evening, when emerging from roost holes in the morning, and during power struggles (Koenig 1981), but such 'pre-roost mounting' is aseasonal, unrelated to age, sex, or status within a group, and does not appear to be a prelude to copulation (MacRoberts & MacRoberts 1976). In contrast, mountings leading to copulation during a female's fertile period are rarely observed. Thus the first question is: what is the function of pre-roost mounting? The second is: where and when does copulation take place? We have no idea concerning the answer to the first of these problems, while the most likely answer to the second is that copulations take place inside roost cavities, although this has yet to be confirmed.

The third, and perhaps most perplexing question, is: why are copulations hidden? One hypothesis is that copulating secretively confuses paternity and facilitates the ability of females to recruit male help in the provisioning of their young (Stacey 1982). Comparative evidence, however, fails to support this conjecture. For example, the cooperatively breeding Florida Scrub-Jay *Aphelocoma coerulescens* is similarly secretive in its mating behaviour but strictly monogamous both socially and genetically (Quinn et al. 1999), whereas copulations in the monogamous and cooperatively breeding Red-cockaded Woodpecker *Picoides borealis* are readily and commonly observed (Haig et al. 1994).

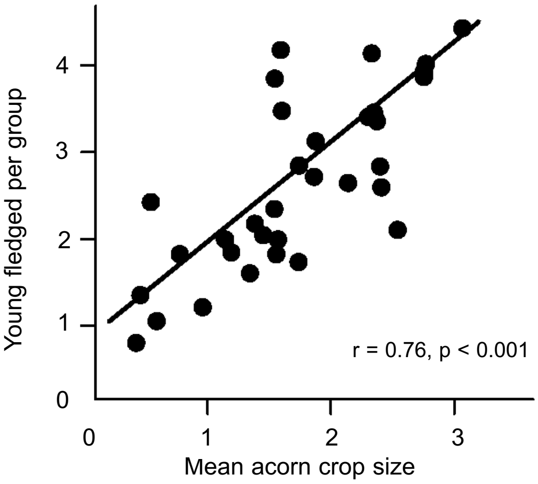

Fig. 2. The correlation between the size of the overall acorn crop (*ln*-transformed number of acorns counted in standardised 30-sec counts on marked trees) and the mean number of young fledged per group the following spring at Hastings Reservation, Monterey County, California, USA. A linear regression is plotted. Data from 1981 to 2013.

One hypothesis is that colonial hole-nesting species may copulate within cavities as a means of reducing interference wheres solitary species copulate outside of cavities where interference is less likely to be a problem (Birkhead et al. 1987). Clearly a more thorough comparative analysis of copulatory behaviour in cooperative breeders is warranted and would be needed to understand the functional significance of this trait.

MORE GENERAL ISSUES

Why do so few secondary cavity nesters use old Acorn Woodpecker cavities?

There is currently considerable interest in woodpeckers as keystone 'ecosystem engineers' excavating cavities that are used by secondary-cavity-nesting species in 'nest-web' communities (Martin & Eadie 1999, Martin et al. 2004, Robles & Martin 2014). In the oak savanna habitat of central coastal California there is a rich community of secondary-cavity nesting species, including Western Bluebirds *Sialia mexicana*, Ash-throated Flycatchers *Myiarchus cinerascens*, Oak Titmice *Baeolophus inornatus*, and Violet-green Swallows *Tachycineta thalassina*, as well as Dusky-footed Woodrats *Neotoma fuscipes*, various mice species (*Peromyscus* spp.), and several other less common species. None of these species appear to commonly use Acorn Woodpecker cavities at our study site, however. Since 1998 we have followed nesting cavities used by Acorn Woodpeckers and recorded nest reuse 271 times over a total of 1283 cavity-years. Of the 488 cases in which apparently useable cavities were reused (38.0% of cavity-years), 325 (66.6% of cases of cavity reuse) were by Acorn Woodpeckers and 120 (24.6% of cavity reuse) were by the introduced European Starling *Sturnus vulgaris*. Species other than these two were recorded using cavities in only 43 cavity-years (8.8% of cavity reuse). The most frequent of these other species was introduced European Honeybees *Apis melifera*, which inhabited cavities previously used by Acorn Woodpeckers in 16 cavity-years (3.3% of cavity reuse), followed by Dusky-footed Woodrats (8 cavity-years, 1.6% of cavity reuse). Bird species, all of which were recorded using cavities on only one or two occasions, included Western Bluebirds, Oak Titmice, Ash-throated Flycatchers, Northern Flickers *Colaptes auratus*, Western Screech-Owls *Megascops kennicottii,* and Saw-whet Owls *Aegolius acadicus*.

Acorn Woodpeckers are by far the most common cavity-excavating species in this habitat. Nonetheless, they appear to be a minor contributor to cavities used by other species in the community with the exception of introduced European Starlings. Why other species fail to take greater advantage of this resource is unclear. One possibility is that the starlings outcompete other species and keep them from using Acorn Woodpecker cavities (Weitzel 1988), but such interference by introduced starlings does not appear to be general (Koenig 2003). Furthermore, old Acorn Woodpecker cavities at our study site frequently go unused even when European Starlings are not present: of previously used nesting cavities that were apparently still useable, 56% were not used for nesting by any species in any one year. Although this does not preclude the possibility that some cavities were used for non-nesting activities such as roosting, it is consistent with the hypothesis that starlings are not a major factor keeping other species from using old Acorn Woodpecker nest cavities for their own use. Alternatively, natural cavities suitable to the various native species may not be limiting, similar to the situation found in some other undisturbed forests such as Białowieża National Park in eastern Poland, where competition for nest sites is of minor importance and woodpecker species are not a keystone provider of cavities (Wesołowski 2007).

What is the adaptive significance of brood reduction?

One advantage of the groups that result from the combination of delayed dispersal by offspring and mate-sharing (polygynandry) is that, with up to a dozen adults feeding at a nest, more nestlings can be raised than if only a pair provisioned young. Indeed, larger groups fledge more young, but brood reduction is still common, with 16% of nestlings perishing due to starvation between hatching and fledging (Koenig & Mumme 1987). Of these, the vast majority — 55 of 72 (76%) followed by Stanback (1991) — perished within 3 days of hatching, and young from eggs that hatch more than 24 h after the first egg hatches almost invariably die, regardless of group size or ecological conditions. In other words, brood reduction was common even in highly productive years following large acorn crops and among large groups with multiple cobreeders and helpers.

Brood reduction is common in birds and generally thought to be related to the dependence on irregular or unpredictable food (O'Connor 1978). Stanback (1991) considered this and other hypotheses for the functional significance of the hatching asynchrony facilitating brood reduction in Acorn Woodpeckers, but concluded that there was little support for any of them. Thus, the selective advantages of hatching asynchrony and brood reduction in Acorn Woodpeckers, if any, remain unknown, despite being a significant factor limiting reproductive success.

How do birds detect reproductive vacancies?

Reproductive vacancies, formed when all breeders of one sex die or disappear, are often followed by intense, prolonged fights among same-sex coalitions of helpers termed 'power struggles' for the opportunity to fill the vacancy and become breeders in the new territory (Koenig 1981). Power struggles can be initiated very rapidly when a vacancy arises, involving dozens of birds, a great deal of vocalising and fighting, and are generally won by the largest participating sibling coalition (Hannon et al. 1985). In some cases, vacancies may be filled in less than an hour: we have observed cases of power struggles initiating within 30 min of dawn after temporary detention of the only breeder of one sex in a group and Hannon et al. (1985) reported one experimental removal in which replacement occurred within 20 min. If helpers of the same sex as the breeding vacancy remain in the group, however, these helpers will often prevent new breeders from joining the group and result in a significant delay in filling the vacancy (Hannon et al. 1985, Koenig et al. 1999).

How do birds detect vacancies so quickly? Hannon et al. (1985) suggested that birds still in the group may advertise for new mates, supporting this hypothesis with evidence that *karrit-cut* calls, a common display often given in conjunction with head-bobbing in response to a variety of stimuli (MacRoberts & MacRoberts 1976), increased on experimental territories following removals. This hypothesis seems unlikely to explain the ability of birds to detect and initiate power struggles within such a short time frame, however, since there would be little opportunity for residents, much less intruders, to assess and respond to a newly-created vacancy within minutes of a bird being removed. We do know that helpers regularly foray off their home territory in search of vacancies (Koenig et al. 1996), and we suspect that they know the birds present on many nearby territories individually and are thus able to quickly assess and detect when a key bird is no longer present and a vacancy may therefore exist.

Once a bird detects a vacancy, his or her best option would presumably be to fill it as quietly as possible before other potential competitors discover and contest it, thereby avoiding a power struggle. We have no way of knowing how frequently this happens, although anecdotally it appears possible that some birds discover that a replacement has taken place — and thus that it is worth contesting a newly-established breeder — even several days after a vacancy has otherwise been filled. One such case involved a singleton female that had filled a vacancy, apparently successfully, without initiating a power struggle, but was then forced out by a coalition of three sisters four days later in a power struggle initiated by the coalition. The singleton female subsequently returned home to her natal group, recruited a sister, returned to the territory with the vacancy, and succeeded in displacing the coalition of three females in collaboration with her sister (Hannon et al. 1985).

This example supports the hypothesis that birds may recognise individuals within groups to the extent that they can tell when a vacancy has been filled and initiate power struggles as a means of contesting a new recruit that is not yet entirely settled. Alternatively, it is possible that birds detecting a vacancy may, at least in some cases, initiate a power struggle as a means of ensuring that the established breeder has indeed disappeared and that a vacancy actually exists. As a third possibility, the remaining breeders may advertise the vacancy, as suggested by Hannon et al. (1985), as a means of inciting competition among potential replacements (Cox & Le Boeuf 1977). Regardless of which mechanism is involved, the detection of vacancies and the initiation of powers struggles involve intriguing behaviours worthy of additional attention.

Does cavity limitation drive cooperative breeding?

There is considerable variability among woodpeckers in the degree to which they excavate new cavities vs. reuse old cavities (Martin 1993), a difference that has a variety of potential fitness consequences in terms of predation rates, parasitism, and the time and energy required to construct a new cavity (Wiebe et al. 2007). As mentioned above, Acorn Woodpeckers frequently (> 50% of the time) reuse old nest cavities and are thus on the 'weak-excavator' side of this continuum. Although this is consistent with the hypothesis that cavities play an important role in limiting the life-history of this species, populations of at least five other species of woodpeckers have approximately equivalent or higher rates of nest reuse, and thus are presumably even weaker excavators, but only one of these — the Red-cockaded Woodpecker — is a cooperative breeder (Wiebe et al. 2006).

As discussed previously, experimental work indicates that cavities play a key role in limiting territory establishment. Why this limitation apparently drives the unusual social behaviour of this species remains unclear, however. In contrast to the special resin-coated cavities used by Red-cockaded Woodpeckers that have been shown to play a key role in the evolution of delayed dispersal and cooperative breeding in that species (Walters et al. 1992), there is no obvious feature of cavities produced by Acorn Woodpeckers that distinguishes them in any special way (Hooge et al. 1999). Differences in the propensity of various species to excavate cavities in different habitats could certainly play a role in social evolution, but has only begun to be investigated either by examining species life histories (Wiebe et al. 2006, 2007) or by comparing different habitats and communities (Cornelius et al. 2008, Cockle et al. 2011).

How did caching behaviour evolve and how is it related to social behaviour?

The California range of Acorn Woodpeckers experiences a Mediterranean climate with generally dry summers and cool, wet winters. In such areas, it makes sense to cache acorns individually in small holes in a way that allows them to dry out despite wet, but typically above-freezing, conditions that would otherwise leave them vulnerable to rot or mould. The range of this species extends as far south as Colombia (Koenig et al. 1995b), however, with the center of its geographic distribution being in the highlands of southern Mexico (Honey-Escandón et al. 2008) where the diversity of oaks is particularly rich (Nixon 1993). In these more tropical regions, the phenology of oaks is likely to be considerably more variable than in temperate regions (Koenig & Williams 1979) and the environmental conditions during the non-breeding season are likely very different from the Mediterranean climate of California. Nonetheless, acorn storage in these regions has been observed, but appears to be neither universal nor necessarily correlated with group living (Dickey & Van Rossem 1938, Miller 1963, Skutch 1969, Koenig & Williams 1979, Ridgely & Gaulin 1980, Kattan 1988). Thus, it is unclear not only how or where the unique caching behaviour of this species evolved, but also the relationship of acorn storage to its complex social organisation. Studies of other social *Melanerpes* species, yet to be conducted, may help address these questions.

What drives the ecological effects of male and female helpers?

Analysis of the fitness benefits of helpers indicates that female helpers have a non-significantly positive effect on the number of young fledged that does not vary with ecological conditions (i.e. the acorn crop) while that of male helpers is linearly related to the acorn crop, being highly positive when the crop is good and slightly negative when poor (Koenig et al. 2011; Figs. 3A,B). These differences are difficult to explain at any level of analysis. Functionally, they beg the question of why most helpers are tolerated by breeders, with the exception of male helpers when the acorn crop is large and conditions are good. Mechanistically, there appears to be no correlation between the fitness effects of helpers and their respective provisioning rates (Figs. 3C,D), and thus it is unclear what mechanism accounts for this positive male helper effect on group reproductive success.

It is possible that the fitness effects of helpers are due to behaviours besides provisioning, although to the extent that such data are available, they similarly fail to parallel the fitness effects of helpers (Mumme & de Queiroz 1985). Clearly there is much to be learned about both the fitness effects of helpers and the proximate mechanisms driving those effects in Acorn Woodpeckers, as well as most other cooperative breeding species.

How important is female mate choice in determining paternity?

We have already discussed the secretive manner in which Acorn Woodpeckers mate, with copulations being rarely observed. Consequently, we have no direct data on whether, or how, females discriminate among potential mates, despite there being high reproductive skew with a single male often siring all the young within a brood (Haydock & Koenig 2002, 2003). We are currently attempting to obtain data on the identity of sperm present on the perivitelline membrane of eggs (Carter et al. 2000) as a proxy for which males have copulated with females, but much remains to be done regarding the role of mate choice and sperm competition in this species.

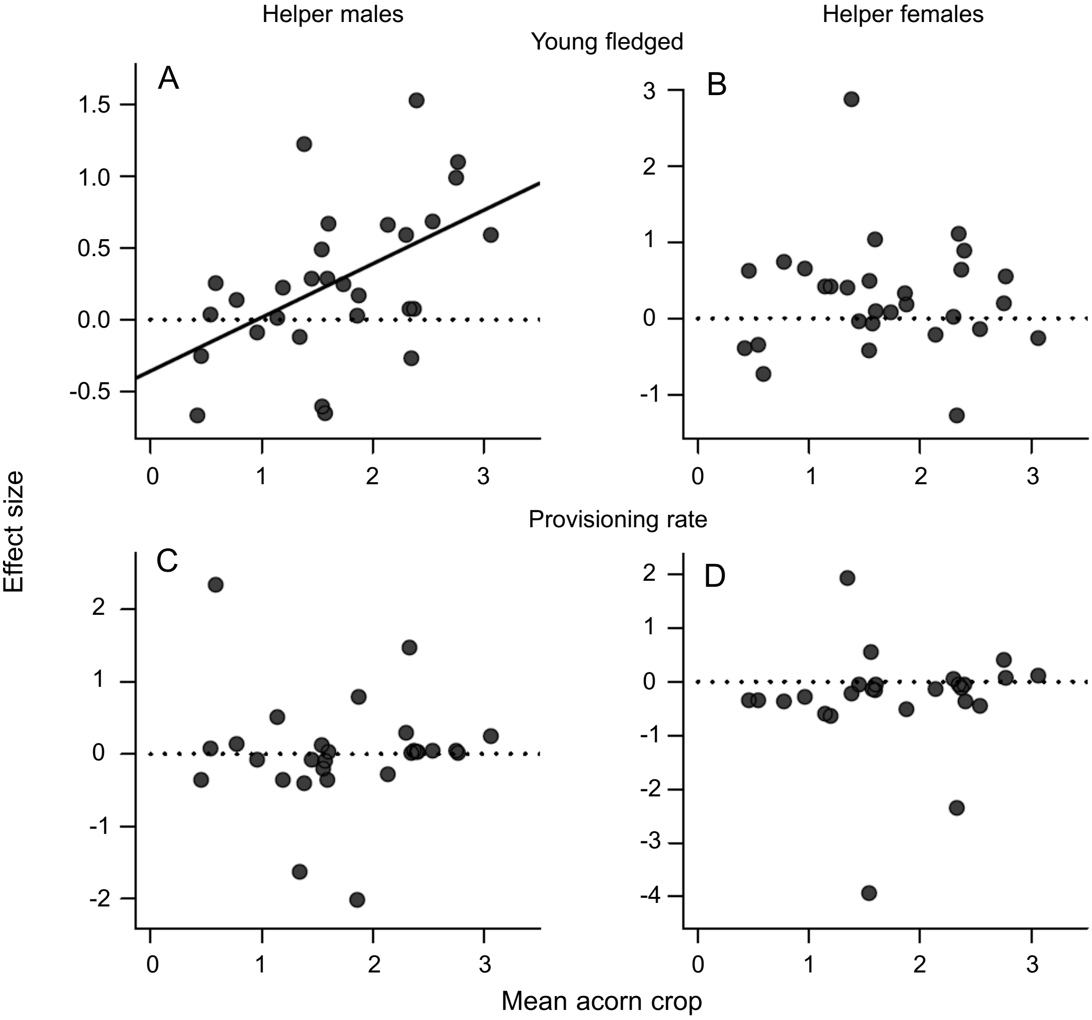

Fig. 3. Top: the indirect fitness benefits (estimated by the number of young fledged) attributable to a single (A) helper male and (B) helper female plotted against the mean size of the acorn crop (Koenig et al. 2011). Bottom: the provisioning rate (standardised for brood size and nestling age) of (C) helper males and (D) helper females plotted against the acorn crop. In all plots, each point is the mean for a year. Only (A) is significant (r = 0.49; n = 29 years; p = 0.007): the fitness effects of a helper male increases with the size of the acorn crop and is slightly negative when the crop is small, whereas the fitness effects of a helper female are non-significant and unrelated to the acorn crop. Provisioning rates are unrelated to the acorn crop for both helper males and females.

Why do females nest jointly?

Typically females will reciprocally destroy each other's eggs, forcing them to nest jointly in order for either to be successful (Koenig et al. 1995a). In 2012, however, we discovered, for the first time, a group whose females apparently nested separately within the territory, with both females provisioning at both nests (E. Walters & W. Koenig, unpublished data). Thus, plural breeding can occur, although it is apparently rare. More generally, however, we do not understand why females generally nest jointly rather than separately. Joint-nesting ensures both synchrony and shared maternity within nests, but entails considerable wasted effort in terms of egg destruction that could potentially be avoided by plural nesting. On the other hand, joint-nesting eliminates the necessity for group members to choose among nests at which to provision, which may ultimately benefit a subordinate female that would otherwise be outcompeted by her joint-nesting relative.

A dominant female could conceivably keep a subordinate from laying eggs entirely within a group if she could recognise her own eggs, but such egg recognition apparently does not occur. Presumably the all-white, relatively indistinguishable eggs of this species are a constraint making it difficult for birds to evolve egg recognition, although additional study is, once again, called for. In any case, we understand very little about why females nest jointly. Geographic variation in this behaviour, although difficult to assess, could potentially shed light on the ecological basis of this problem.

DISCUSSION

There are many more questions to be answered than there is time, energy, or funds to address in a complex species like the Acorn Woodpecker. We suspect that a similar list of questions could be made for almost any species, although no doubt several of the unique aspects of Acorn Woodpeckers make this task particularly easy in our case. Indeed, we believe that some of the most important benefits of long-term studies — in addition to the demographic data that can be acquired and the quantification of otherwise difficult-to-study factors such as lifetime fitness and linkage across generations (Fitzpatrick & Woolfenden 1981) — are the opportunity to observe responses to environmental changes, the ability to discover and observe phenomena that may initially appear to be rare but illustrate unexpected behavioural plasticity, and the chance to digest the potential significance of behaviours whose function is not immediately obvious. Long-term population studies are difficult to fund and maintain (Birkhead 2014), but provide unique opportunities to test hypotheses for the adaptive significance of many behaviours and to gain perspective of a sort that cannot be achieved in short time-frames or by alternatives such as space-for-time investigations (Clutton-Brock & Sheldon 2010).

There are, of course, pitfalls to studying the same population for an extended period of time. As pointed out by Cohen (1976), there is always the possibility that we are chasing ‘nondegenerate limit random variables’ that converge over time, but to an arbitrary value with no ecological or functional significance. If we were to start a second study of a population of Acorn Woodpeckers in a parallel universe that was identical to the one we’ve studied at Hastings Reservation, would we generate comparable demographic data, come to similar conclusions, and have the same set of unanswered questions? Our guess is probably not, although we suspect that we would generate equally interesting sets of conclusions and questions, just as studies of the same species have frequently revealed intraspecific differences, both in Acorn Woodpeckers (Koenig & Stacey 1990) and in vertebrates generally (Lott 1991).

The bottom line is that there is much to be gained by in-depth, long-term studies, not just in terms of answering the questions one might have had initially, but by generating questions that could not possibly have been asked when the study was started. For example, we have observed enormous changes in molecular methods over the past four decades, allowing questions of relatedness to be asked today that were impossible to address in the 1970s. Some of these new questions will potentially lead to novel ideas that will likely alter our prior perspectives. Indeed, a unique advantage of a long-term study is that it provides one with the opportunity to revise one’s thoughts about the factors that are important to the population as one has the opportunity to observe and study it under differing ecological conditions and using newly developed techniques.

In the case of the Acorn Woodpecker, we offer the above list as a starting point for a future woodpecker student (or more generally of animal behaviour) looking for interesting unanswered questions to study. We trust they will answer at least some of them, no doubt generating their own list of even more perplexing questions in the process.

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STRESZCZENIE

[Czego jeszcze nie wiemy o gniazdującym kooperatywnie dzięciole — dzieciurze żołędziowym]

Dzięciur żołędziowy jest jednym z niewielu gatunków dzięciołów, u którego stwierdzono lęgi kooperatywne. Żyje on w grupach składających się z maksymalnie 15 osobników obu płci i charakteryzuje się dość skomplikowanym systemem rozrodczym. Wiedza o tym gatunku jest dość rozległa, głównie dzięki ponad 40 letnim badaniom prowadzonym w Kalifornii, jednak nadal jest wiele niezbadanych aspektów jego biologii. W pracy wiele z takich zagadnień jest omówionych w szerszym kontekście, wraz z sugestiami przyszłych badań. Przedstawione zagadnienia są pogrupowane od relatywnie szczegółowych pytań interesujących z punktu widzenia gatunku, takich jak dlaczego ptaki dorosłe mają jasne tęczówki lub dlaczego młode osobniki przypominają upierzeniem dorosłe samce (Fig. 1), aż do problemów bardziej ogólnych, jak związek dostępności miejsc gniazdowych z ewolucją specyficznych zachowań socjalnych, czy adaptacyjne znaczenie redukcji lęgu u gatunku z pomocnikami gniazdowymi. W tym ostatnim kontekście interesujące są pytania o wpływ dostępności pożywienia (zmagazynowanych żołędzi) na liczbę piskląt (Fig. 2), czy zależności pomiędzy płcią pomocników lęgowych a liczbą wyprowadzanych piskląt przez grupę dzięciurów (Fig. 3).

Autorzy podkreślają, że szczególnie wartościowe są badania długoterminowe, które nie tylko dają nam możliwość odpowiedzi na wiele ciekawych pytań, ale co ważniejsze — generują kolejne pytania, które mogłyby być przeoczone bez szczegółowej wiedzy o biologii badanego gatunku.