

## LETTERS

## Parochial altruism in humans

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**Social norms and the associated altruistic behaviours are decisive for the evolution of human cooperation<sup>1–9</sup> and the maintenance of social order<sup>10</sup>, and they affect family life, politics<sup>11</sup> and economic interactions<sup>12</sup>. However, as altruistic norm compliance and norm enforcement often emerge in the context of inter-group conflicts<sup>13,14</sup>, they are likely to be shaped by parochialism<sup>15</sup>—a preference for favouring the members of one's ethnic, racial or language group. We have conducted punishment experiments<sup>16</sup>, which allow 'impartial' observers to punish norm violators, with indigenous groups in Papua New Guinea. Here we show that these experiments confirm the prediction of parochialism. We found that punishers protect ingroup victims—who suffer from a norm violation—much more than they do outgroup victims, regardless of the norm violator's group affiliation. Norm violators also expect that punishers will be lenient if the latter belong to their social group. As a consequence, norm violations occur more often if the punisher and the norm violator belong to the same group. Our results are puzzling for evolutionary multi-level selection theories based on selective group extinction<sup>2–5</sup> as well as for theories of individual selection<sup>17–19</sup>; they also indicate the need to explicitly examine the interactions between individuals stemming from different groups in evolutionary models.**

The human species is unique in the extent to which it regulates social life with normative obligations that constrain selfish behaviour<sup>1,20</sup>. Social norms such as food sharing, or those related to cooperative hunting and participation in warfare, shaped human life throughout important evolutionary phases<sup>1,21–23</sup>. It is therefore likely that the existence of these norms had a deep impact on the properties of human altruism, because norm obedience and norm enforcement involve important altruistic behaviours. The fact that social norms are group level phenomena<sup>24</sup> suggests that parochial social instincts<sup>15,25</sup>—which we define as preferences for favouring the members of one's own social group—may have shaped human altruism in decisive ways. Norms emerge through interactions in groups and apply to interactions within groups; group members enforce them, and they often arise in the context of inter-group conflicts<sup>13,14</sup>. Normative obligations are thus likely to apply only to ingroup members; people who do not belong to the group neither obey the norm nor benefit from the altruistic behaviours the norm enforces.

In this paper, we study the potentially parochial nature of altruistic norm enforcement by conducting third-party punishment experiments<sup>16</sup> with members of two small, distinct, cohesive and non-hostile indigenous groups in the Western Highlands of Papua New Guinea (PNG)—the Wolimbka and the Ngenika. Centralized institutions for the enforcement of legal rules are largely absent in PNG, meaning that social norms almost exclusively regulate social life. In addition, PNG societies more closely resemble the human societies under which our social instincts evolved than the modern, complex societies in which most people at present live. PNG is therefore an ideal environment for studying the parochial nature of human altruism.

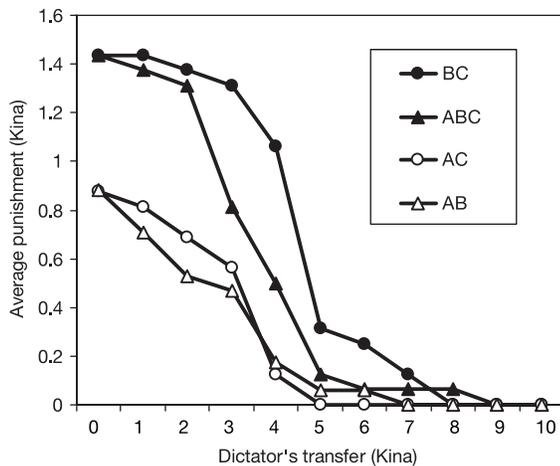
The use of cohesive, indigenous groups from simple societies distinguishes our study from minimal group experiments<sup>26,27</sup> based on artificially created laboratory groups of students. Researchers have found some forms of ingroup favouritism in simple allocation experiments based on the minimal group paradigm. However, the ingroup favouritism observed in these experiments<sup>26,27</sup> does not reveal parochial tendencies in human altruism because the subjects only distributed resources between two other subjects. Subjects thus bore no cost, regardless of how they allocated the available resources between the other two subjects. Moreover, subsequent research<sup>28,29</sup> has shown that costless ingroup favouritism in these experiments is due to the expectation that ingroup members will receive some reciprocation from other ingroup members. Thus, what looked like a preference for ingroup favouritism was in fact based on the expectation of ingroup reciprocity<sup>29</sup>.

In our study, we conducted an anonymous, one-shot, third-party punishment experiment<sup>16</sup> involving a dictator (player A), a recipient (player B) and a third party (player C). Player A receives an endowment of 10 Kina (K), which is equivalent to a high daily labourer's wage in the informal sector of the economy. Player B, the recipient, has no endowment and player C, the third party, receives K5. First, A can transfer any amount between K0 and K10 to B. Then C is informed about A's transfer and has the opportunity to punish A's action by spending K0, K1 or K2 on punishment. Every Kina spent on punishment reduces A's income by K3. After player A and C had chosen their actions, we also elicited their expectations about how the dictators would be punished at the three transfer levels K0, K5 and K10.

Our experiment is designed to capture the altruistic enforcement of egalitarian sharing norms that ethnographic studies have documented<sup>22,30,31</sup>. Such sharing norms are beneficial for the group because they insure group members against the uncertainties in individual food acquisition success. If an egalitarian sharing norm exists, we should observe both that dictators transfer money to the recipients and that third parties exhibit altruistic punishment<sup>7</sup> for transfer levels below the equal split. As we wanted to examine the parochial behavioural patterns, we allocated each subject in our study to one of the following four treatment conditions. (1) All three players in the game are from the same tribe (treatment ABC). (2) Only players B and C are from the same tribe, while A is an outgroup member (BC). (3) Only players A and B are from the same tribe (AB). (4) Only players A and C are from the same tribe (AC). The decision-makers in all four treatments were informed about the other two players' group affiliation.

Current evolutionary models based on the idea that human altruism evolved through the selective (cultural or biological) extinction of groups in inter-group conflicts<sup>2–5</sup> predict the following punishment pattern. No punishment should be observed in treatment AC if A does not share, because there is no obligation to share with a recipient B from the outgroup. Sharing with an outgroup member would only help the competing group, possibly at the

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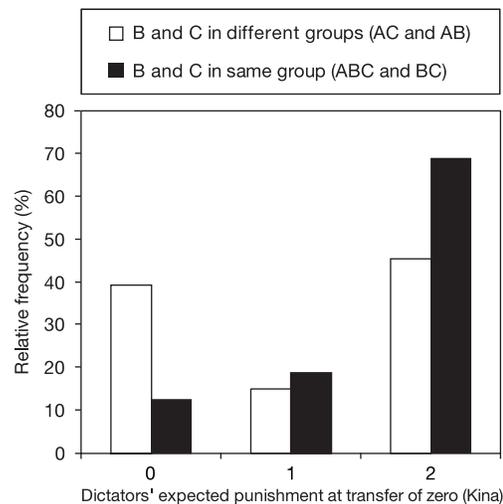


**Figure 1 | Punishment pattern across conditions in the third-party punishment game.** The third party spends money (Kina) on punishing the dictator for the violation of an egalitarian sharing norm in all conditions. Punishment expenditures by third parties increase if dictators reduce transfers below the egalitarian sharing norm; punishment is highest in all conditions if the dictator does not share at all. Punishment expenditures are much higher in the ABC condition, where dictator (A), recipient (B) and third party (C) belong to the same group, than in the AB condition (where only the dictator and the recipient belong to the same group) and the AC condition (where only the dictator and the third party belong to the same group). Contrary to predictions, punishment is also much higher in the BC condition (where the recipient and the third party belong to the same group) than in the AB and the AC condition.

expense of the ingroup. The same punishment prediction is made for condition AB, where the third party is an outgroup member; in this case A violates a sharing norm if she or he does not share with B, but player C—being an outgroup member—has no obligation to punish a norm violation within the other group. Likewise, the group competition theories predict zero punishment in condition BC because A is an outgroup member who is not obliged to obey a sharing norm in interactions with an ingroup member. Thus, the ABC treatment is the only condition in which evolution should have favoured altruistic punishment, because punishment in ABC sustains group norms that enhance a group's ability to compete with other groups.

We observe that the punishment pattern is qualitatively similar in all four treatment conditions (Fig. 1). There is little punishment for transfers at and above the egalitarian level, while sharing decisions that give the dictator a larger share of the 'pie' are more heavily punished the more the dictator deviates from the equal split. For example, even in the conditions with relatively low punishment levels (AB and AC), 58% of the third parties punish if the dictator transfers nothing, but only 3% punish at K5 and nobody punishes at transfers higher than K6. This finding suggests the existence of an egalitarian sharing norm in all four conditions, and not just in the ABC condition—a fact that is puzzling in view of the predictions above. The third parties' and the dictators' beliefs further support this interpretation. Regardless of the treatment condition, individuals in both roles believe that a transfer of K0 will be punished severely, while transfers of K5 or K10 will not be punished.

Although punishment of low transfers is not zero in the AB and the AC conditions, the size of the punishment across the ABC, the AC and the AB condition obeys the order that selective extinction models<sup>2–5</sup> predict: punishment is much higher when all three players belong to the same group (ABC) compared to the AC and the AB treatments, where punishment is roughly the same (Fig. 1). The difference between ABC and the other two treatments is highly significant (ordered probit regression,  $P = 0.007$ , two sided,  $N = 539$ ), while the difference between the AC and the AB conditions



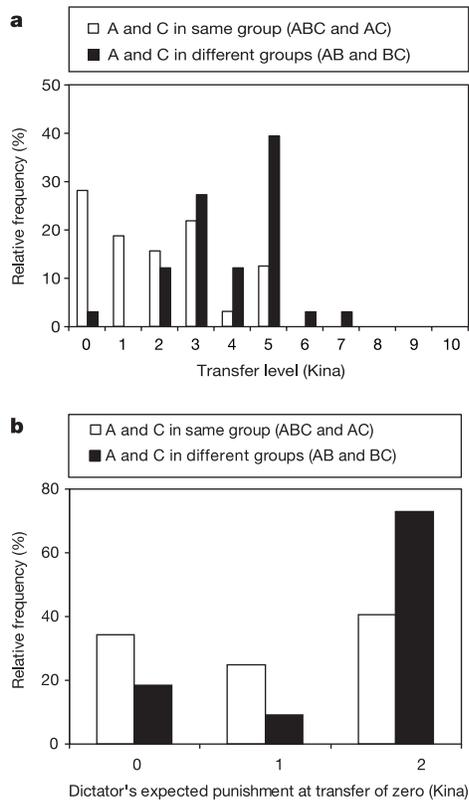
**Figure 2 | The punishment threat for the lowest transfer level as perceived by the dictators.** The punishment threat subjectively perceived is important, because higher expectations about punishment induce more compliance with the sharing norm. In those conditions where the recipient (B) and the third party (C) belong to the same group (that is, in conditions ABC and BC), dictators perceive a higher punishment threat than in conditions where B and C belong to different groups (that is, in conditions AB and AC).

is negligible and insignificant (ordered probit regression,  $P = 0.947$ , two sided,  $N = 539$ ; see also statistical methods in Supplementary Information).

Punishment in the BC condition is also much higher than in the AC and the AB conditions (Fig. 1; ordered probit regression,  $P < 0.001$ , two sided,  $N = 539$ ). Controlling for the transfer level, the probability that the third party punishes a violation of the sharing norm is 30.4 percentage points higher in the BC condition than in the AC and AB conditions. In fact, punishment in BC is even significantly higher than in ABC (Fig. 1; ordered probit regression,  $P = 0.022$ , two-sided,  $N = 352$ ). The difference between these two conditions is particularly large at transfer levels of K3 and K4. For example, the average punishment at a transfer level of K4 is more than twice as high in BC than in ABC. Thus, third parties are more lenient if the norm violator belongs to their group.

These findings imply that regardless of the dictator's group affiliation, punishment is much higher if the recipient and the third party belong to the same group. Thus, to the extent to which third-party punishment deters potential norm violators, the victims of potential norm violations are much more protected by the threat of third-party punishment if the third party belongs to the victim's group. The dictators' expectations also support this deterrence effect of third-party punishment. The dictators expect significantly more punishment at K0 in those conditions where B and C belong to the same group (Fig. 2; ordered probit regression,  $P = 0.019$ , two sided,  $N = 65$ ), and the expected punishment level at K0 has a significantly positive effect on transfer levels. A one-unit increase in expected punishment raises the transfer level by 1.43 units (tobit regression,  $P < 0.001$ , two-sided,  $N = 65$ ). Thus, both actual punishment and punishment expectations suggest that victims of norm violations are much more protected if the victim and the third party belong to the same group.

How do these punishment patterns, together with the parochial pattern of voluntary norm compliance, shape the transfer levels? We find that the transfers are higher in those conditions where A and B belong to the same group (tobit regression,  $P = 0.018$ , two-sided,  $N = 65$ ). The dictators even transfer more money in these conditions if we control for their punishment expectations (tobit regression,  $P = 0.086$ , two-sided,  $N = 65$ ). Thus, dictators who expect the same



**Figure 3 | Dictators' transfers and perceived punishment threats if the third party belongs to the dictator's group. a**, Relative frequency of dictators' transfer decisions. Dictators comply much less with the egalitarian sharing norm if the third party belongs to their group. **b**, Relative frequency of dictators' perceived punishment threats in the case of a transfer of zero. Dictators believe that they will be punished much less if the third party belongs to their group.

level of punishment give more in those conditions where A and B belong to the same group, suggesting a higher degree of voluntary norm compliance in these treatments (see also statistical methods in Supplementary Information).

Player A's reluctance to share if B does not belong to his group is strongly reinforced if the third party comes from A's group. In this case the dictators' transfers are substantially lower on average compared to the conditions where A and C belong to different groups (Fig. 3a; tobit regression,  $P < 0.001$ , two-sided,  $N = 65$ ). Moreover, the punishment threat subjectively perceived is significantly lower if the third party belongs to the dictator's group (ordered probit regression,  $P = 0.022$ , two sided,  $N = 65$ ). For example, only 41% of the dictators expect the maximal punishment at a transfer of K0 if the third party is from their group, but 73% of the dictators expect the maximal punishment if the third party is from the other group (Fig. 3b). Thus, dictators expect that 'their' third parties will be lenient, inducing them to transfer little to the recipient.

Although our findings are puzzling from the viewpoint of current selective extinction models<sup>2-5</sup>, they also suggest how the models could be extended in order to explain the full empirical pattern. First, these models focus on norm enforcement within groups for the purpose of winning inter-group conflicts while neglecting the potential benefits from cooperative inter-group interactions. This approach makes it difficult to understand when hostility characterizes inter-group reactions and when cooperative norms govern them. The current models therefore have problems in explaining our first main result—the existence of egalitarian sharing norms in all four conditions—but a suitably extended model, which explicitly formalizes individual strategies in inter-group encounters, may be able to

capture this fact. Second, the lack of explicit modelling of individual inter-group encounters makes it also difficult to understand why—regardless of the norm violator's group affiliation—punishment is so high in those conditions where the third party and the recipient (ABC and BC) belong to the same group. Punishing outsiders who harm an ingroup victim increases the general security of all ingroup members by preventing attacks by outgroup members. If a group has a reputation for punishing individual attacks by outgroup members, the latter are deterred from such attacks and all ingroup members enjoy more protection. Thus, taking the problem of group reputation into account could possibly explain the high punishment in both the BC and the ABC conditions.

Current individual selection models<sup>17-19</sup> also cannot readily explain the full pattern of punishment behaviours. Models based on repeated interactions or reputation formation<sup>9,18,19</sup> seem to predict that punishment will be highest in the ABC condition, because the third party's reputational benefits from punishing are most favourable in this condition: protecting an ingroup victim may yield a future ally and punishing an ingroup violator lessens the likelihood of being cheated in future interactions with the norm violator. Kin selection theory<sup>17</sup> is also not fully satisfactory, because the average genetic relatedness between two randomly selected adult tribe members in tribes of several hundred people is rather low, due to migration and marriages with outgroup members. It is therefore difficult to see why kin selection should have favoured a sharing norm that applies to all tribe members alike—in particular in situations such as our experiment, where the dictator's fitness loss already exists for other reasons, kin selection might have favoured a lower punishment of ingroup members, which could explain the lower punishment in ABC compared to the BC condition.

Thus, if future research confirms the robustness of our results, the parochial patterns of human altruism constitute a challenge for existing evolutionary theories. Currently, no single theory seems to be able to explain the entire pattern of parochialism across treatments, providing an opportunity for developing new theories or modifying existing ones.

## METHODS

**Subjects.** A total of 195 members—aged 17 to 60—of two small-scale societies in the Western Highlands of PNG (the Wolimbka and the Ngenika) participated in a third-party punishment game, permitting us to conduct 65 games with three players each. We conducted 17 games in the AB treatment and 16 in each of the other treatments.

Tribal warfare is a frequent event in PNG, but the Ngenikas and the Wolimbkas never conducted tribal warfare with each other within the memorized history of the older members of the two tribes. They are neutral towards each other and do not exchange any gifts or goods, except in the rare case of inter-tribe marriage. Due to the absence of any hostilities between the two tribes, finding parochialism across these two tribes makes our results even stronger.

**Experimental procedures.** Game instructions and procedures are based on the work of Henrich *et al.*<sup>32</sup>. In each experimental session, 18 participants first received some preliminary verbal instructions as a group. We ensured that the participants did not communicate about the game before the experiment. Each participant received a show-up fee of K3 and drew a number at the beginning. One at a time, in the order of the pulled numbers, the subjects then came into a separate room to participate in the experiment. The game was then explained to them verbally in much detail. Participants who failed to understand the instructions were dismissed from the experiment but could keep their show-up fee.

We elicited player C's punishment decision with the strategy method (see Supplementary Information). This means that player C indicated how much he or she is willing to spend on punishment for each of player A's feasible transfers. Player C made this decision before (s)he knew the dictator's actual transfer level. Since we collected 11 punishment decisions from each player C—one punishment decision for each feasible transfer level—we always controlled for repeated measurement in the statistical analysis of punishment decisions.

**Statistical methods.** The punishment decisions were examined with ordered probit regressions. We controlled for repeated individual measurements and for individuals' transfer levels in all regressions. Treatment effects were measured by dummy variables that take on a value of one if the observation comes from the

treatment of interest. Otherwise the dummy variable is zero. The dictators' transfer decisions were analysed with tobit regressions that consider the transfer level as a function of the expected punishment and the treatment dummies of interest.

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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## Original Article

# Delayed dispersal in western bluebirds: teasing apart the importance of resources and parents

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Delayed and localized dispersal are fundamental life-history traits associated with formation of family groups and kin neighborhoods. Although the field has focused mainly on resource benefits and ecological constraints as drivers of delayed dispersal, social benefits of nepotism can also be important. Resources and nepotism are theoretically correlated as the affordability of nepotism scales with resource abundance. Rarely have both been analyzed simultaneously within a single analysis. Western bluebird sons (*Sialia mexicana*) stay in family groups on mistletoe-based territories for winter, disperse locally to form kin neighborhoods in spring, and have a low level of facultative helping by sons, brothers, and grandsons. Although a son's tendency to remain on the natal territory increased with the number of parents present, mistletoe volume on the natal territory was a good predictor of sons staying home only for groups where the mother alone was present. Overwinter survival of sons was exceptionally high (95%) such that neither resources nor parental presence predicted survival advantages during the first year of life. When sons stayed on their natal territory for winter, their spring presence increased with the volume of mistletoe on their winter territory and was higher if they wintered with at least 1 parent. Stay-at-home sons acquired a portion of their parents' territory in spring, including mistletoe that scaled with their parents' mistletoe wealth. Our results indicate that although resources are undoubtedly important for the maintenance of family ties, the importance of maintaining connections with parents is underappreciated in studies of cooperative breeding.

**Key words:** benefits of philopatry, cooperative breeding, delayed dispersal, ecological constraints, kin neighborhood, prolonged brood care.

## INTRODUCTION

The most common form of cooperative breeding occurs when offspring delay dispersal and help at their parents' nests (Brown 1974; Emlen 1978). Although delayed dispersal and helping usually go hand-in-hand, there is growing evidence that they are not tightly coupled (Ekman et al. 2004; Stern 2012; Akcay et al. 2013). Highly flexible associations among kin are now known for a variety of territorial and colonial cooperative breeders (Curry and Grant 1990; Emlen and Wrege 1992; Hatchwell and Russell 1996). When young settle locally, they can return home to help (redirected helping) and, in some species, individuals even have nests of their own while helping (Dickinson and Akre 1998). This variation makes it possible to analyze benefits of prolonged association with relatives and the natal territory (or nest) independent of the benefits

of helping, empirically separating fitness consequences of helping from the social and ecological drivers of delayed dispersal.

Why are the benefits of delayed dispersal so important to understanding the evolution of cooperative breeding? We tend to frame kin-based cooperative breeding in terms of the inclusive fitness consequences of delayed dispersal, delayed breeding, and helping (Brown 1987; Emlen 1978). This decision-tree framework has expanded to include all possible options, such as floating and usurping (Koenig et al. 1992; Cahan et al. 2002). Based on demographic analysis, only rarely does selection favor remaining home simply in order to help (Ekman et al. 2004; but cf. Stacey and Ligon 1987; Heinsohn 1991; Covas and Griesser 2007) and, when opportunities arise, helpers usually prefer to breed (Pruett-Jones and Lewis 1990; but cf. Komdeur 1992). The rarity of cases in which helping compensates for failing to breed underlies Cockburn's (1998) suggestion that helping is an epiphenomenon of delayed dispersal. If families are inherently unstable (Emlen 1995), offspring must gain social or ecological benefits from staying in their natal groups, living in kin

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neighborhoods, and engaging in prolonged interactions with their parents and other relatives (Hatchwell 2010; Stern 2012). In other words, kin-biased helping may simply be a form of opportunism that derives from the social and material benefits of living near parents or on the natal territory.

Treatments of cooperative breeding have largely pointed to either environmental variance, both spatial and temporal (Emlen 1982; Stacey and Ligon 1991; Russell and Rowley 1993; Cockburn and Russell 2011), or ecological constraints (Emlen 1982; Brown 1989) as primary drivers of delayed dispersal in natural populations. Although environmental variance is easily measured, predictions based on constraints are usually species specific (Kokko and Ekman 2002) and have been experimentally tested in only a few altricial bird species (Pruett-Jones and Lewis 1990; Copeyon et al. 1991; Komdeur 1992; Covas et al. 2004). Basic properties of group living, such as group defense against predators, do not require the young to stay home and, thus, are not really benefits of delayed dispersal per se. In Red-cockaded Woodpeckers, *Picoides borealis*, a high-quality natal territory and an abundance of high-quality territories within 1 km are associated with the tendency of offspring to stay-and-foray, whereas offspring from territories with significant sib competition and a high concentration of vacant territories within 3.5 km are more likely to adopt a depart-and-search strategy (Pasinelli and Walters 2002). These results point to the possibility that offspring assess prospects for gaining a breeding vacancy nearby versus farther away in deciding whether to stay or go.

When young stay home, they gain access to space, food, and shelter, and these benefits can be augmented by familiarity and nepotism (Ekman et al. 1994; Ekman, Baglione, et al. 2001). In the Siberian jay, *Perisoreus infaustus*, offspring delay dispersal for up to 3 years and never help at the nest (Ekman, Eggers, et al. 2001) but gain increased survival through nepotistic food sharing, vigilance, mobbing, and alarm calling (Griesser 2003; Griesser and Ekman 2004, 2005; Griesser et al. 2006). The alternative to delayed dispersal is traveling through unfamiliar or inhospitable habitat and bearing the socially mediated costs of entering a new neighborhood and an unfamiliar social group (Woolfenden and Fitzpatrick 1978). By staying home, offspring can gain increased access to breeding space and mates through inheritance or territorial budding (Woolfenden and Fitzpatrick 1978), but they may also pay countervailing costs due to local breeding competition (Dickinson 2004a).

In central coastal California, USA, western bluebird pairs defend territories year-round, and sons commonly stay home through their first winter (Kraaijeveld and Dickinson 2001). Dispersal is female biased both prior to and after spring, as is typical for passerine birds (Greenwood and Harvey 1982; Ekman et al. 2004), but sons frequently remain in their family groups until their second spring, and many acquire territories nearby. The majority of sons breed as yearlings, but some delay breeding without helping (floaters); help at the nests of their parents, brothers, or grandfathers; or act as replacement males at nests of widowed females (Dickinson and Weathers 1999). Fitness measures indicate that helping is inferior to independent breeding, not only for helper sons, which get a small, noncompensatory, indirect fitness benefit from helping, but also for their parents, whose inclusive fitness would be increased if their sons bred rather than helped (Dickinson 2004a). Often helpers have attempted to breed and failed, having lost their mate (Dickinson and Akre 1998; Dickinson 2004a). The benefits of delayed and localized dispersal have yet to be identified, but resources (e.g., oak mistletoe, *Phorodendron villosum*) (Dickinson and McGowan 2005)

and social factors, such as parental nepotism or “prolonged brood care,” are potentially important (Ekman et al. 2004; Dickinson et al. 2009).

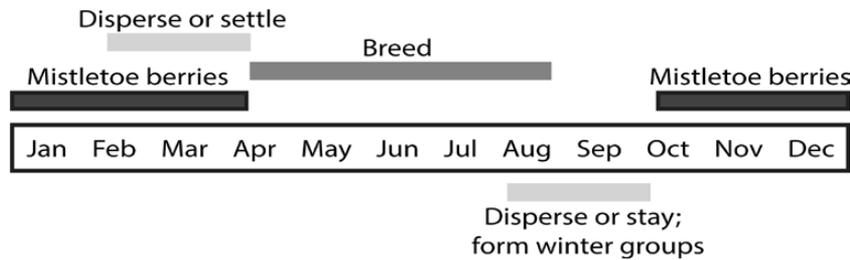
In our study area, partial (50%) removal of a single ecological resource, oak mistletoe, led to a sharp decrease in the frequency of delayed dispersal of western bluebird sons (Dickinson and McGowan 2005). Because most parents still wintered on their territories after mistletoe was removed, we inferred that sons were induced to disperse because mistletoe resources were scant, even though dispersing meant leaving their parents behind. This does not necessarily mean that extended interactions with parents are not beneficial. In winter, mothers, in particular, are less aggressive to sons and daughters at mealworm feeders than to immigrant young of the year and young birds feed at higher rates when living with parents than with unrelated adults (Dickinson et al. 2009). Delayed dispersal can be viewed as a transaction between parents and offspring over access to resources. Although offspring have more to gain by remaining with parents on territories with abundant resources, parents also pay a lower fitness cost of conceding resources to young on high- than low-resource territories (Ekman and Rosander 1992). In cooperatively breeding banded mongooses (*Mungos mungo*), parents evict offspring when the costs of allowing them to remain on the natal territory are too high (Cant et al. 2001). Findings like these point to the importance of examining the effects of resources and parents within the same analysis.

Here, we report on social and resource drivers of delayed dispersal in western bluebirds, based on a rare effort to track 5 cohorts of a year-round resident bird population from when young fledged, through the winter, and into their first breeding season. We analyze the importance of social, ecological, and demographic drivers as well as the consequences of delayed dispersal and local settlement 1) during the fall dispersal period when sons stay home, leave to join nearby groups for winter, or leave the study area altogether; 2) over winter, when survival consequences of mistletoe abundance and parental presence can be compared; 3) in spring, when surviving first-winter males either settle locally or leave the study area; and 4) after settlement, when breeding status and within-pair and extrapair fertilizations can be assessed. By quantifying resource abundance and accounting for parental presence in the same analysis, we were able to examine the interaction between social and resource drivers of delayed dispersal throughout a male's first year of life.

## MATERIALS AND METHODS

### Study population

This research is based on a long-term study of western bluebirds at Hastings Reserve, the adjacent Oak Ridge Ranch, and Rana Creek Ranch in upper Carmel Valley, CA. Western bluebirds exhibit 2 sequential periods of natal dispersal (Figure 1). The first period occurs in late summer, prior to the formation of stable territorial groups, and the second occurs after winter when birds remain locally or disperse elsewhere to breed (Kraaijeveld and Dickinson 2001). Western bluebird groups defend mistletoe-based territories vigorously during the nonbreeding season and are especially aggressive to same-sex conspecifics (Kleiber et al. 2007). When faced with a combination of related and unrelated first-winter birds in their groups, mothers, but not fathers, are more tolerant of sons and daughters than of unrelated individuals joining their group (Dickinson et al. 2009).



**Figure 1**

The annual cycle of western bluebirds in central coastal California, showing the 2 periods of dispersal relative to the fruiting of mistletoe. Pairs are territorial year-round and young of the year either stay at home or disperse in late summer–early fall when winter groups form. Groups are stable until early spring, when first-winter birds move out of groups and onto territories to breed.

### Monitoring, mapping, winter group composition, and mistletoe abundance

Our research methods are consistent with ASAB/ABS procedures and were covered under Animal Care and Use Permits #R212 at UC Berkeley and #2005-0137 at Cornell University. Basic methods for monitoring in spring are given in Dickinson et al. (1996). Briefly, all breeding birds and nestlings in our study area were color banded from 1983 until present. In fall of 2001, we began to census a subset of winter groups and in fall of 2002, we added systematic winter censuses of all territories occupied in spring for a total of at least 3 h of censuses per month per territory from September until the end of February. This protocol continued through winter 2005–2006, representing 5 years of censusing. Winter censuses were used to determine group composition and group size, which were highly stable after 1 October. Individuals were assigned to a group if they were seen at least once in that winter group. If they were seen in more than 1 group, they were assigned to the group they were most often seen with. (This is rare but happens when feeding sites are located at territorial boundaries.)

We collected data on mistletoe volume for 3377 geolocated mistletoe-bearing Valley Oak (*Quercus lobata*) and Blue Oak (*Quercus douglasii*) trees using a 1.25-m reference stake. We classified each clump into 5 size categories using the formula for the volume of a sphere with radius 10, 20, 35, 60, and 75 cm and summed to obtain a total mistletoe volume ( $m^3$ ) for each tree. Clumps measuring  $>1.5$  m in diameter fell into a sixth size category; they tended to be elongated and were estimated as one or more smaller clumps (Dickinson and McGowan 2005). Mistletoe volume was calculated relative to the central nest-box or winter group box as the summed volume over all trees within a 100-m radius.

Territory mapping was conducted during winter censuses in winter of 2004 and near nests in spring of 2005. Territory maps were created in ArcGIS10 based on combined independent data points placed on the map during periodic visits in combination with points obtained during 1–2 h focal pair or winter group watches. The territory boundary was the minimum convex polygon using 100% of the points, excluding points involving territorial intrusions by the focal bird, which elicited a chase by the neighboring bird. A pair's mistletoe holdings included the trees found within the minimum convex polygon.

### Classification of first-winter males and females

Birds were aged by molt limit (Shizuka and Dickinson 2005) or were of known age based on having been banded as nestlings. We classified first-winter birds as “natal” if they were on or near their natal territory with one or both parents present in their winter groups

or if their parents were no longer present, but the sons were on their natal territory with relatives that were not their parents. It was important to allow for slight movements because fathers and sons occupying adjacent territories in spring sometimes coalesced into 1 group for winter. If a bird was off its natal territory in a new group that did not include its parents, it was considered to have “moved groups.” Because siblings sometimes disperse together, we allowed nonnatal groups to include siblings or more distant relatives. Birds not previously banded, but appearing in winter groups for the first time and having a molt limit, were considered immigrant first-winter birds. Both “moved” and “immigrant” males were considered “nonnatal” for most analyses. Only males that “moved” could be used in comparisons involving both the natal territory and the winter territory.

### Calculating future within-group mating opportunities

We used individual-specific operational sex ratio (OSR) as a proxy for potential access to future mates, first accounting for incest avoidance by assuming that a male would not mate with a bird of relatedness  $\geq 0.25$ . We subtracted the OSR in the male's winter group from that on his natal territory, adding the focal male to the number of males in his natal group in order to capture what the OSR would have been had the son stayed home for winter.

### Overwinter survival analysis

We used a standard Cormack–Jolly–Seber mark-recapture model (Lebreton et al. 1992) to determine the survival of first-year males over the course of the winter based on the 3 separate census periods: September/October, November/December, and January/February during winters beginning in 2001–2005 and ending in 2006. Any bird present during at least one of these 3 census periods was counted as being alive prior to surveying, having survived since fledging the prior spring. We did not include survival past the end of February because western bluebirds enter a second phase of dispersal in early spring when a subset of males leaves the study area (Figure 1). Including presence in spring in the survival analysis would thus conflate death with dispersal.

First, we tested whether survivorship was a function of natal status (natal vs. nonnatal group) and mistletoe resource availability. We did not distinguish immigrants from birds that moved to new groups in the study area because, given the movement within the study area, the geometry of our large study area, and the substantial edge of the area, most immigrants of unknown origin likely came from just off the study area and thus could not be reliably distinguished from those we knew to have moved groups. We modeled the effect of several potential explanatory variables on winter

survival ( $\psi$ ) and detection probability ( $\rho$ ), including winter group size as a categorical covariate, standardized winter mistletoe volume ( $z$ -score) as a covariate, and whether first-winter males wintered in their natal group versus a nonnatal group as an unordered categorical variable. In this case, the nonnatal classification included males that moved to new groups and immigrant males of unknown origin that entered groups other than their natal group.

We treated winter group size and winter mistletoe volume as group-level categorical covariates. Winter group sizes were aggregated into 4 levels based on the data: <5, 5–7, 7–9, and >9. Mistletoe was also aggregated at 4 levels as follows:  $\leq -0.83$ ,  $-0.83$  to  $-0.35$ ,  $-0.35$  to  $0.40$ , and  $0.40$ – $3.28$ . We developed a targeted set of candidate models testing the influence of winter group size and winter mistletoe volume on overwinter survival. In addition, we tested for a seasonal effect by including time of season for each model. The model set included the null  $\psi(\cdot)$   $\rho(\cdot)$  testing for constant survivorship and detectability across the winter season. We evaluated these models using an information-theoretic approach and calculated  $AIC_c$  (Akaike information criteria),  $\Delta_i$   $AIC_c$  differences ( $\Delta_i$ ), and Akaike weights ( $w_i$ ) for each model. Models with a  $\Delta AIC_c$  less than 2 were considered to be equivalent and strongly supported given the data (Burnham and Anderson 2002). Survival analysis was performed in the R version statistical platform version R2.14.2 for Windows XP (R Development Core Team 2011) using the Rmark package (Laake et al. 2012).

### Local settlement in spring

We used a generalized linear mixed-effect model (GLMM, binomial distribution) to test the effect of mistletoe holdings and parental presence on sons' presence in spring (McCulloch et al. 2008). GLMM models included the detection/nondetection of males in spring as a response variable. Fixed effects included wintering in the natal group (or not) as a fixed factor. Arcsine square root of the OSR and mistletoe volume ( $m^3$ ) on the natal territory were covariates and winter group size and OSR were numerical covariates. Winter year was nested within winter group ID and treated as a random effect.

### Paternity analysis

We used previously published data on parentage in the analysis of spring reproductive success. Methods for paternity assignment using microsatellite typing are described in detail in 2 previous papers (Ferree et al. 2010; Ferree and Dickinson 2011).

### Statistical analysis

All statistics were run in R2.13.1 for MAC, except for the survival analysis, which was run in Rmark on Windows XP in R2.14.2 (R Development Core Team 2011). All errors given are the standard error of the mean. Sample sizes varied due to missing values for one or more variables. For example, when analyzing the effect of parents on delayed dispersal, a test of 0 versus "at least 1" parent would have a higher sample size than a test of 0, exactly 1, and exactly 2 parents, because "at least 1 parent" allows for uncertainty about whether there were 1 or 2 parents. Further, a subset of the 2001 breeding boxes was not available to be sampled the following winter due to land access issues, so fledglings from those areas were excluded from analysis of detection in winter groups after the first period of dispersal, but could be included as "movers" in analyses of overwinter survival and presence after the second period of dispersal, given that their identities and nests of origin were known. We alert the reader to the fact that detection probability in our

MARK analysis bears no statistical or conceptual relation to probability of detection in winter groups or as breeders in spring.

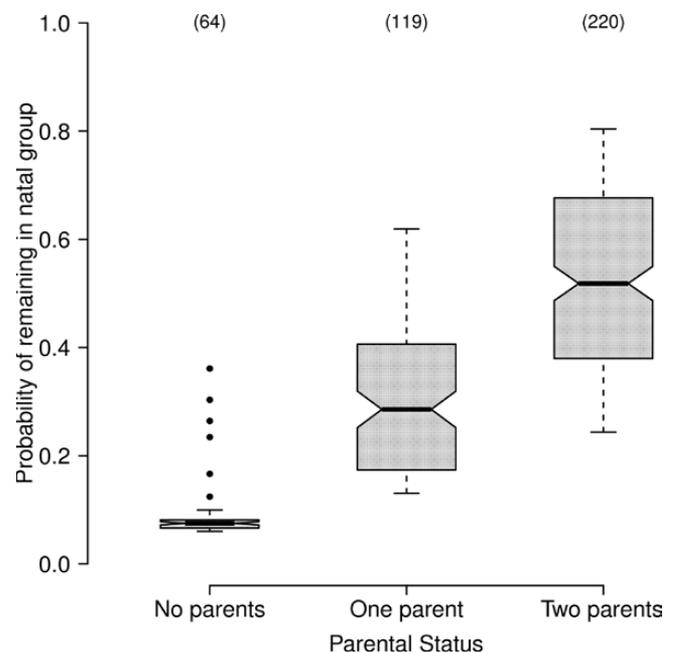
## RESULTS

### First period of dispersal

#### *Effect of mistletoe and parents on presence in the natal group in winter*

The amount of mistletoe within 100 m of the natal nest-box was a good predictor of the volume within 100 m of the central nest-box on sons' winter territories (Pearson's  $r = 0.90$ ,  $N = 165$ ,  $P < 0.001$ ) and this volume, in turn, was positively correlated with the volume falling within the winter territory boundaries for 10 winter territories that were extensively mapped in 2004–2005 (Pearson's  $r = 0.86$ ,  $N = 10$ ,  $P < 0.002$ ). In contrast, we found no significant correlation between natal and winter mistletoe volumes for sons that moved to new groups (Pearson's  $r = -0.37$ ,  $N = 14$  winter groups,  $P = 0.17$ ). Mean area was  $38488 \pm 4025$   $m^2$  for 38 distinct winter group territories. A circle with a 100-m radius was used to include years and territories not mapped because of the aforementioned correlation and because its area of 31400  $m^2$  is close to halfway between the mean (38488  $m^2$ ) and the median (25995  $m^2$ ) for winter territories.

Of 409 sons that fledged in 2001–2005, 165 (40%) overwintered in their natal groups and 15 (4%) moved to new territories in the study area. The remaining 229 (56%) dispersed or died, whereas 29 first-winter males joined winter groups from off the study area. We observed a significant stepwise increase in delayed dispersal with 0, 1, and 2 parents present in winter groups (Figure 2; parents: GLMM,  $\beta = 1.22$ ,  $N = 403$ ,  $z = 5.84$ ,  $P < 0.001$ ). Mistletoe volume on the spring territory was not a good predictor of delayed dispersal, nor was the interaction between parents and mistletoe volume statistically significant (mistletoe volume: GLMM,  $\beta = 0.08$ ,  $N = 403$ ,  $z = 0.23$ ,



**Figure 2** Results of GLMM: Probability of remaining in the natal group for first-winter male western bluebirds with no parents present on the study area compared with those with 1 and 2 parents present.

$P = 0.82$ ; interaction:  $\beta = 0.01$ ,  $N = 403$ ,  $z = 0.07$ ,  $P = 0.94$ ). Mothers were previously shown to be nepotistic at feeding stations, whereas fathers were not (Dickinson et al. 2009). The probability of detection of sons in the natal group in winter increased with mistletoe volume when mothers alone were present, but not when fathers alone were present (GLMM, binomial, mothers:  $\beta = 0.66$ ,  $N = 76$ ,  $z = 2.36$ ,  $P = 0.02$ ; fathers:  $\beta = -0.64$ ,  $N = 76$ ,  $z = -1.28$ ,  $P = 0.20$ ).

Sons that left their natal groups and joined new groups on the study area did not disperse to higher mistletoe-volume territories than they were born on (mean difference =  $-26.5 \text{ m}^3$ ,  $z = -1.86$ ,  $N = 19$ ,  $P = 0.08$ ); sons with parent(s) present were less likely to move groups than were sons without parents (GLMM, binomial:  $\beta = 2.79 \pm 0.62$ ,  $N = 162$ ,  $z = 4.5$ ,  $P < 0.001$ ). In summary, we found consistent support for an effect of parental presence on delayed dispersal, but the effect of mistletoe volume was restricted to cases where only the mother was still present.

### Sensitivity to future indirect (kin selected) or direct fitness benefits

As predicted if future indirect benefits are important, sons were more likely to remain in their natal group when they had 2 parents than 1 parent present (GLMM, binomial:  $\beta = 0.86 \pm 4.73$ ,  $N = 339$ ,  $z = 3.33$ ,  $P = 0.001$ ). Sons that moved to new groups rarely had parents present and were no more likely to have 1 parent (9% of 44 males moved) than 2 parents present (3% of 118 males moved) (Fisher's Exact test:  $P = 0.21$ ). When sons moved to nonnatal groups on the study area, the group they moved to did not have a more favorable sex ratio for pairing than did their natal group, had they stayed home (paired  $t$ -test: natal OSR – new OSR, mean difference = 1.1,  $t = 1.27$ ,  $N = 11$ ,  $P = 0.24$ ).

## Fitness consequences of delayed dispersal

### Survival of males as a function of mistletoe abundance and wintering with parents

RMARK analysis resulted in 64 models testing the influence of overwinter survival probability as a function of group size, winter mistletoe volume, and continued association with at least 1 parent. We did not find support for models of survival that included mistletoe volume or group size as explanatory covariates (Table 1). Beyond slight seasonal variation in overwinter survival, the only factor that tended to have support was group-level differences between natal and nonnatal males; however, these differences were slight in light of the overall high winter survival probability of both groups. For all first-winter males, winter survival probability was high across the winter season (September–February:  $\psi(\cdot) = 0.95 \pm 0.010$ ).

**Table 1**  
Model selection table for winter survival and detection probability of first-year males

Model	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
$\Psi_{(f)} P_{(nat+f)}$	7	572.4	0.00	0.55
$\Psi_{(f+nat)} P_{(nat+f)}$	8	573.7	1.34	0.28

Survival was modeled as a function of  $\psi$ , winter survival probability, and  $\rho$ , detectability, based on condensing 3–4 censuses per month to presence or absence during summer and three 2-month periods stretching over fall and winter. We present  $K$ , the number of estimable parameters;  $AIC_c$ , the Akaike information criteria, a measure of each model relative to the best model;  $\Delta AIC_c$ ; and  $w_i$ , the Akaike weight of evidence. All models with a  $\Delta AIC_c < 2$  are shown. The explanatory variable, nat, refers to whether an individual was in its natal group or not.

Overwinter survival ( $\psi$ ) demonstrated a slight decrease for natal males as the winter season progressed, declining from  $0.95 \pm 0.020$  to  $0.89 \pm 0.048$  and remained relatively unchanged for nonnats ( $0.99 \pm 0.002$ ). Detection probability ( $\rho$ ) was also high for natal males ranging from  $0.82 \pm 0.03$  in early winter to  $0.93 \pm 0.02$  in midwinter and  $0.92 \pm 0.04$  in late winter. For nonnatal males, detection probability was lowest in the beginning of the winter season when some immigrants were unbanded ( $0.47 \pm 0.07$ ) and peaked during the middle of winter ( $0.75 \pm 0.06$ ). Analysis of immigrants compared with “movers” revealed no differences in survival or detectability between these 2 groups across the season.

## Second period of dispersal

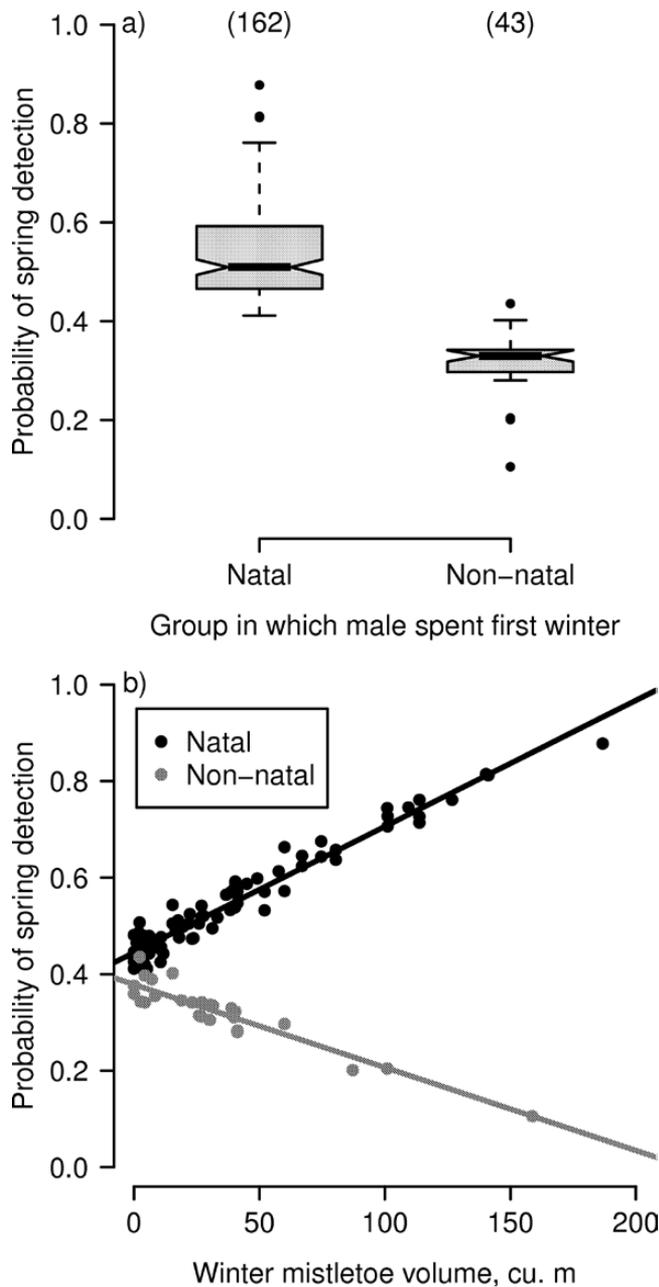
### Effect of mistletoe volume and parents on presence of surviving sons in spring

Of the 209 first-winter males overwintering on the study area in 2001–2006 (5 winters), we observed 103 (49%) on the study area the following spring. Of these, 60% were breeders, 14.5% were helpers, 7% were paired without nesting, 1 (1%) was a replacement male at a nest of a widowed female, and 17% were observed, but of unknown status (floaters or breeders just off the study area). Parental presence (natal/nonnatal) and winter mistletoe volume were strong predictors of presence on the study area in spring for sons surviving their first winter (GLMM, binomial: natal vs. nonnatal,  $\beta = -1.09 \pm 0.40$ ,  $z = -2.72$ ,  $N = 201$ ,  $P = 0.007$ ; mistletoe volume,  $\beta = 0.47 \pm 0.19$ ,  $N = 201$ ,  $z = 2.44$ ,  $P = 0.015$ , Figure 3a,b). The interaction between parental presence and mistletoe volume on the winter group's territory was also significant (GLMM, binomial:  $\beta = -0.92 \pm 0.46$ ,  $N = 209$ ,  $z = -1.99$ ,  $P = 0.046$ ).

Males that wintered with parent(s) were more likely to disperse locally after winter than were males that joined a new group for winter (Figure 3a). Localized dispersal in spring increased with mistletoe volume for sons overwintering on their natal territories and decreased for sons that moved to new groups for winter. Neither OSR (GLMM, binomial:  $\beta = -0.03 \pm 0.85$ ,  $N = 201$ ,  $z = -0.04$ ,  $P = 0.97$ ) nor group size (GLMM, binomial:  $\beta = -0.02 \pm 0.05$ ,  $N = 201$ ,  $z = -0.40$ ,  $P = 0.69$ ) was a significant predictor of sons' local presence in spring. Sons that stayed on their natal territories for winter were no more likely to remain on the study area in spring if they had 2 parents than if they had just 1 parent still alive (Fisher's Exact test:  $P = 0.41$ ,  $N = 161$ ), nor were sons more likely to remain home in spring when only their mothers were present than when only their fathers were present (GLMM, all  $P > 0.5$ ).

### Effect of mistletoe and parents on tendencies to breed and fledging success in spring

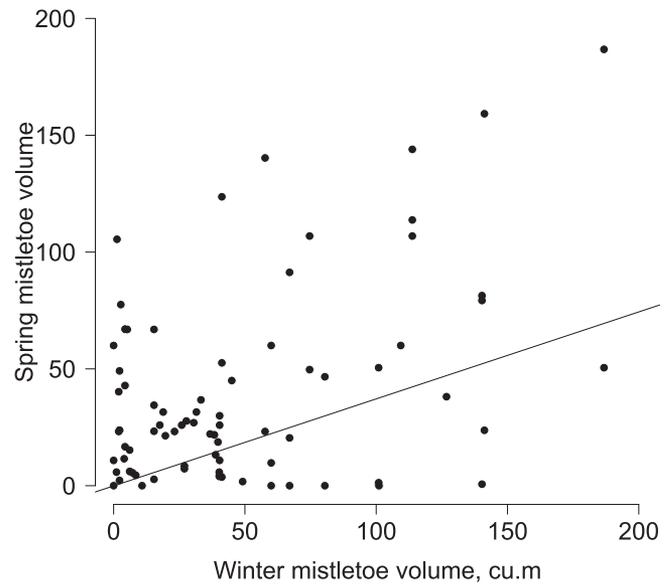
When the winter group's OSR was male biased, males were less likely to breed and more likely to adopt one of the nonbreeding options (e.g., helping) (GLMM, binomial:  $\beta = -2.48 \pm 1.24$ ,  $N = 100$ ,  $z = -2.01$ ,  $P = 0.04$ ); other predictor variables including group size, mistletoe, parental presence, and interactions had no statistical support ( $N = 100$ ,  $z < |1.13|$ ,  $P > 0.25$ ). Neither winter mistletoe volume ( $\text{m}^3$ ), wintering in the natal group, nor winter group size influenced postwinter fledging success for yearling males breeding on the study area (GLMM, binomial, mistletoe volume:  $\beta = -0.12 \pm 0.22$ ,  $z = -0.55$ ,  $N = 100$ ,  $P = 0.58$ ; natal/nonnatal:  $\beta = -0.05 \pm 0.69$ ,  $N = 100$ ,  $z = 0.07$ ,  $P = 0.29$ ; group size:  $\beta = -0.07$ ,  $N = 100$ ,  $z = -1.06$ ,  $P = 0.29$ ). The number of extra-pair offspring sired by yearling males ( $N = 4$  offspring in all years) was too few to influence delayed dispersal.



**Figure 3**  
Results of GLMM: (a) Probability of detecting surviving yearling males in spring as a function of whether they wintered in their natal group or a nonnatal group on the study area. (b) Probability of detecting surviving yearling males in spring as a function of mistletoe volume on the winter territory when they wintered in their natal groups (black line and dots) versus in nonnatal groups (gray line and dots).

### Resource consequences of delayed dispersal: territorial budding

When sons overwintered on their natal territory, the volume of mistletoe within 100 m of the central nest-box on their winter territory was a good predictor of the volume of mistletoe within 100 m of their spring nest-box (GLMM:  $\beta = 0.37 \pm 0.09$ ,  $N = 83$ ,  $z = 4.07$ ,  $P < 0.001$ , Figure 4). We also examined more precisely the resource holdings for 10 first-winter sons whose group territories were mapped in winter of 2004–2005 and whose breeding territories were also



**Figure 4**  
Results of GLM: Relationship between mistletoe volume within 100 m of central nest-box on the natal territory during winter and the mistletoe volume within 100 m of the son's nest-box the next spring.

mapped in spring of 2005. Sons nesting next to their parents after winter acquired  $15 \pm 4\%$  standard error (SE) (4–34%) of the group's winter territory. A mean of  $65 \pm 12\%$  SE (3–100%) of the sons' spring territory had been part of the group's winter territory. Sons also acquired a mean of  $32 \pm 7\%$  SE (5–67%) of the winter group's mistletoe wealth. Mistletoe acquired by budding off a portion of the winter territory amounted to  $81 \pm 11\%$  SE (36–100%) of the total mistletoe volume yearling males had on their territories in spring.

### DISCUSSION

According to our results, mistletoe and parents differentially influence delayed and localized dispersal (Table 2). Parental presence was associated with increased retention of sons on their natal territories for winter and with tendencies for sons to settle locally in spring. In contrast, delayed dispersal increased with mistletoe volume only when mothers alone were present and was not otherwise a statistically significant predictor of delayed dispersal. This is in contrast with results of our mistletoe removal experiment in which removing half the mistletoe on spring territories led to a sharp decrease in delayed dispersal (Dickinson and McGowan 2005). After winter, mistletoe volume was a good predictor of localized dispersal of sons that stayed home, and of the volume of mistletoe locally dispersing sons would have on their own territories.

As predicted based on future indirect fitness benefits of helping, retention of sons in the natal group increased substantially when sons had both parents present and less so with 1 parent present (Figure 2). This is consistent with our past findings that males in the population were more than 9 times as likely to help when both parents were alive than when 1 parent was alive (Dickinson et al. 1996), although they did not make finer-tuned adjustments to their helping effort based on full- or half-sib relatedness or extrapair paternity (Dickinson 2004b).

Our measures of survival were based on extensive winter censusing, which allowed us to see that most first-winter birds survived right up to the point where spring dispersal occurs, thus ruling out

**Table 2**  
**Main conclusions for effects of resources and parents based on analyses of the 2 periods of dispersal in western bluebirds**

Phase of dispersal and settlement	Response variable	Mistletoe volume	Parent(s)	Criteria for parents
Period 1: Delayed dispersal and winter group formation in August–September based on experiment (Dickinson and McGowan 2005)	Presence in natal group for winter and presence on study area	Reducing mistletoe by half decreased delayed dispersal of sons	No effect on presence of parents on winter territory	Not manipulated
Period 1: Dispersal and winter group formation in August–September	Presence in natal group in winter <sup>a</sup>	No effect with all data; positive effect when mother is present (mother = nepotistic parent)	Positive effect, increasing with <i>N</i> parents	0, 1, or 2 parents
Period 1: Moving groups within the study area	Parents in natal group in winter <sup>a</sup>	No significant effect	More likely to stay home with both parents present	Parents versus no parents
Overwinter: survival once in groups	RMARK survival estimates	No significant effect (95% survived)	No significant effect (95% survived)	Parents versus no parents
Period 2: Postwinter settlement on the study area versus dispersal	Present/absent after surviving winter	Positive effect when wintered on natal territory; otherwise, no effect	Positive effect	Son with 1 or 2 parents versus none
Breeding versus nonbreeding options	Present/absent; breed/not breed	No effect	No effect	Natal versus nonnatal group
Reproductive success in first breeding season	Fledging success	No effect	No effect	Natal versus nonnatal group
Volume of mistletoe acquired in spring	Mistletoe volume within 100 m of son's nest-box in spring	Positively associated with volume on natal, winter territory	Not considered	Included only males wintering with parents <sup>b</sup>

<sup>a</sup>Also supported with smaller data set that included only surviving individuals and whether they stayed home or moved groups.

<sup>b</sup>Eighty-one percent of the mistletoe sons acquired on mapped territories came from their parents' winter territory.

mortality as a cause of disappearance in early spring. Overwinter survival of first-winter males (estimated at 95%) was far higher than reported for either tropical or temperate forest birds (Karr et al. 1990). Our measures also exceeded annual survival estimates based on long-term studies of cooperatively breeding birds (Emlen 1982; Rowley and Russell 1990), although such estimates could be artificially depressed in the absence of winter survival data, because birds leaving during a second stage of dispersal would be counted as dead. Two other recent studies have uncovered relatively high annual survival in delayed dispersers. In Siberian Jays, 79.4% of delayed dispersers survived their first year, whereas first-year survival was about 67% for offspring that dispersed out of their natal group (Griesser et al. 2006). In Gray Jays, *Perisoreus canadensis*, first-winter survival in high-quality habitat was estimated at about 67%, lower than our estimates for first-winter birds in this study, and decreased to about 59% in lower quality habitat with fewer conifers and more pronounced roadside effects (Norris et al. 2013). Survival was so high and invariant in our study that there was little opportunity for differential mortality based on mistletoe volume or parental presence.

Why was survival of first-winter males so high in winter? One possibility is that winter group membership is socially regulated to maintain relatively uniform per capita mistletoe abundance. Our mistletoe removal experiment showed a dramatic increase in dispersal of sons away from the study area after mistletoe on their natal territories was reduced by half, but per capita mistletoe volume was not statistically different from controls, even after new, immigrant females joined the winter groups (Dickinson and McGowan 2005). Winter group formation may obey the ideal free distribution in which the balance of immigration and emigration leads to relatively low variance in per capita resource abundance (Fretwell and Lucas 1970). Also, our experimental removal reduced mistletoe volume far below the mean observed in this study: our spring

territories in this study had a mean of  $70.7 \pm 11.1$  m<sup>3</sup> of mistletoe (0–291 m<sup>3</sup>), whereas the removal territories in our experiment had a mean of  $40.0 \pm 8.1$  m<sup>3</sup> of mistletoe (5.8–89.6 m<sup>3</sup>). By removing half the mistletoe, we may have pushed most removal territories below the threshold level of mistletoe for retention of sons. In the absence of removal, territories and group membership appear to interact in a way that rarely leads to a threshold effect.

Siberian jays are the leading example of combined benefits of nepotism and territory quality generating survival advantages for delayed dispersers (Griesser et al. 2006). Our failure to find such advantages in the first winter, even though fitness benefits of parents and mistletoe should be most obvious in winter, suggests that variation in mistletoe abundance is not relevant to winter survival at the geographic scale of our study area. Overall, mistletoe abundance in the absence of removal is generally high enough to support families with retained sons, a conclusion that is supported by the high survival of retained sons we observed over 5 winters. This is consistent with the assertions of Koenig and Pitelka (1981) that delayed dispersal and, ultimately, cooperative breeding in acorn woodpeckers (*Melanerpes formicivorus*) in central coastal California are associated with low variance in territory quality. This is in direct contrast with findings for Seychelles warblers (*Acrocephalus sechellensis*) and acorn woodpeckers in New Mexico, in which high variance in territory quality can tip the balance such that benefits of helping relative to breeding favor delayed dispersal and helping (Stacey and Ligon 1987; Komdeur 1992). At Hastings Reserve, both western bluebirds and acorn woodpeckers have behaviors that reduce variance in food supplies over the winter. In western bluebirds, this is effected by maintaining mistletoe-based territories, whereas in acorn woodpeckers, resource availability is modulated by the birds' behavior of placing large numbers of acorns into well-defended storage trees or "granaries" (Koenig and Mumme 1987).

Our hypothesis that the habitat is generally of high quality for western bluebirds is supported by research showing that mistletoe trees are spatially aggregated over the maximum detectable distance within the study area (724 m) using the variogram method, which only detects aggregation up to half the distance from one end of the study area to the other (Wilson E, Dickinson JL, Sullivan PJ, unpublished data). In western bluebirds, mistletoe seeds appear in 100% of winter fecal samples (Dickinson and McGowan 2005). Although birds steal berries from territories of neighbors that have left for watering sites, territorial boundaries are otherwise well established (Dickinson JL, unpublished data). Only once in many years of winter research did a group appear to exceed the resource capacity of its territory in winter; this group of 13 birds left for about 1 month in December and then returned with all members in January (Dickinson JL, unpublished data), suggesting that western bluebirds can shift between mobile and territorial lifestyles for short periods, while still keeping their family groups intact.

Within our long-term study site, natural variation in mistletoe volume appears to be more important to localized dispersal than to delayed dispersal. When sons delayed dispersal, their tendency to settle on the study area after winter was highly sensitive to both parental presence and mistletoe volume. Sons wintering on a high-mistletoe-volume territory with their parents were more likely to be present in spring, bred on higher mistletoe-volume territories, and, when nesting next door to their parents, acquired on average 81% of their spring mistletoe volume by budding off a portion of their parents' territory. The percentage of their parents' mistletoe that they gained by budding was lower than the percentage of area their parents conceded, suggesting that parents concede inferior sections of their winter territories to sons. Still, as mistletoe volume on the spring territory is a good predictor of winter territory quality, sons settling locally from high volume territories acquire more mistletoe, which in turn means they have some mistletoe to rely on as they enter their second winter. These findings suggest that the benefits of mistletoe wealth, should they exist, will be seen in longer term measures of survival and reproductive success of philopatric sons, although fall dispersal data indicate that western bluebirds do not necessarily share with Red-cockaded Woodpeckers the trait of electing to stay the winter based on future, local breeding potential (Pasinelli and Walters 2002).

Neither mistletoe nor staying with parents affected the likelihood of breeding or the number of young sired and fledged by sons present in spring. The only predictor variable with fitness consequences in spring was the OSR of the winter group. When males spent the winter in a group with a male-biased OSR and were on the study area in spring, they were less likely to breed and, instead, adopted one of the lower-fitness, nonbreeding options. This apparent shortage of females represents a cost of delayed dispersal and can be explained by tendencies of first-winter males to breed with immigrant females that have joined their winter groups (Kraaijeveld and Dickinson 2001).

Our main results, together with previously published evidence (Dickinson and McGowan 2005), lead to 2 primary conclusions. The first is that mistletoe and access to parents are important determinants of delayed dispersal during both fall and spring dispersal periods, but in fall, the effect of mistletoe is less straightforward and is seen only with 50% removal (Dickinson and McGowan 2005) or when mothers alone are present (this study). Most importantly, parents concede both space and mistletoe to offspring, which may have long-term fitness consequences for sons. Sons not remaining with their parents for winter have a low probability of remaining on the

study area in spring. Staying with parents for winter thus means that sons are less likely to bear the costs of travel to a new location in either fall or spring while also avoiding the uncertainty and aggression costs of entering a new group or neighborhood (Dickinson et al. 2009). Sons that leave their parents behind, whether before or after winter, lose the opportunity to help when they are unable to breed, do not rejoin parents for winter, and will not benefit from cryptic cooperation with extraterritorial relatives (Stern 2012). Despite the recent emphasis on cooperation among nonrelatives, helpers only help relatives in 75% of species with helpers at the nest (Riehl 2013). The central role that parental presence plays in this system adds to a growing body of evidence that the benefits of kin-directed social behavior are more important to delayed dispersal than previously thought and provides fodder for further analysis of the fitness consequences of staying home with relatives and of the costs of dispersal.

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