



# Kinship and familiarity mitigate costs of social conflict between Seychelles warbler neighbors

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**Because virtually all organisms compete with others in their social environment, mechanisms that reduce conflict between interacting individuals are crucial for the evolution of stable families, groups, and societies. Here, we tested whether costs of social conflict over territorial space between Seychelles warblers (*Acrocephalus sechellensis*) are mitigated by kin-selected (genetic relatedness) or mutualistic (social familiarity) mechanisms. By measuring longitudinal changes in individuals' body mass and telomere length, we demonstrated that the fitness costs of territoriality are driven by a complex interplay between relatedness, familiarity, local density, and sex. Physical fights were less common at territory boundaries shared between related or familiar males. In line with this, male territory owners gained mass when living next to related or familiar males and also showed less telomere attrition when living next to male kin. Importantly, these relationships were strongest in high-density areas of the population. Males also had more rapid telomere attrition when living next to unfamiliar male neighbors, but mainly when relatedness to those neighbors was also low. In contrast, neither kinship nor familiarity was linked to body mass or telomere loss in female territory owners. Our results indicate that resolving conflict over territorial space through kin-selected or mutualistic pathways can reduce both immediate energetic costs and permanent somatic damage, thus providing an important mechanism to explain fine-scale population structure and cooperation between different social units across a broad range of taxa.**

kin selection | mutualism | territoriality | telomeres | social conflict

In nature, conflict between individuals occurs because organisms are selected to pursue selfish interests that rarely align with those of the individuals with whom they interact. Conflict can be mitigated by kinship if there are indirect genetic benefits of promoting genes shared with a relative (1). However, conflict resolution can also be achieved if interacting individuals gain direct benefits (either mutualistic or reciprocal) from cooperating with each other (2).

Understanding whether and how conflict is resolved within families, groups, and societies is important for understanding a wide range of behavioral phenomena (3), but it is often unclear if and when kin-selected or mutualistic pathways to conflict resolution are important in animal societies. The respective influences of kinship and mutualistic benefits on conflict resolution could be simultaneous or even interactive (4); both could also be dependent on other aspects of the social environment (5). Furthermore, the degree to which these processes mitigate the observed costs of conflict may depend on the timescale over which those costs are measured. The benefits of reduced conflict between individuals may be observable only after repeated interactions over a long period of time (6).

One area where both kin-selected and mutualistic processes might play important interacting roles is in the resolution of conflict over territorial space. Territoriality is widespread throughout the animal kingdom (7) and is not specific to a particular social system or population structure. Territory boundary defense is

costly (8), so cooperative maintenance of a boundary should be beneficial, as it reduces the need for costly policing. Kin selection could help prevent escalated conflict over territory boundaries, but there is also a well-established mechanism by which mutualistic benefits between interacting individuals could resolve conflict. The “dear enemy” phenomenon predicts that conflict is lower between familiar neighbors (9). This is because it is less costly to maintain territory boundaries with existing neighbors, with whom agreements about territory boundaries have already been reached, than to renegotiate territory boundaries with new neighbors (10). Thus, familiarity between neighbors can be used as a proxy for mutualism-based conflict resolution.

The costs of territoriality do indeed appear to be moderated to some extent by both kinship and familiarity. Individuals living in close proximity to kin in “kin neighborhoods” (11) often have higher reproductive success, which has largely been attributed to reduced aggression toward the offspring of related neighbors (12–14; reviewed in ref. 15). There is also evidence that familiarity between neighbors decreases territorial aggression (16) and improves reproductive success (17, 18). However, several unanswered questions hinder our understanding of conflict resolution in this widespread social phenomenon. First, the respective influences of kinship and familiarity are rarely studied simultaneously in the same system, so conclusions about their relative importance in minimizing territorial conflict and the degree to which they

## Significance

**In nature, animals must compete with their neighbors for access to limited resources. Since conflict over resources can be extremely costly in terms of time, energy, and reproductive success, investigating how individuals resolve conflict is crucial to understanding the evolution of social behaviors. In the Seychelles warbler, we demonstrate two mechanisms by which individuals minimize costs of conflict and show the benefits individuals gain from doing so. Birds that live near relatives or familiar individuals invest less energy in defending and maintaining territory borders and also show less aging-related signs of physiological damage. Our results suggest that conflict between neighbors can be mitigated by kin-selected benefits of sharing resources with relatives but also through direct mutual benefits of cooperation.**

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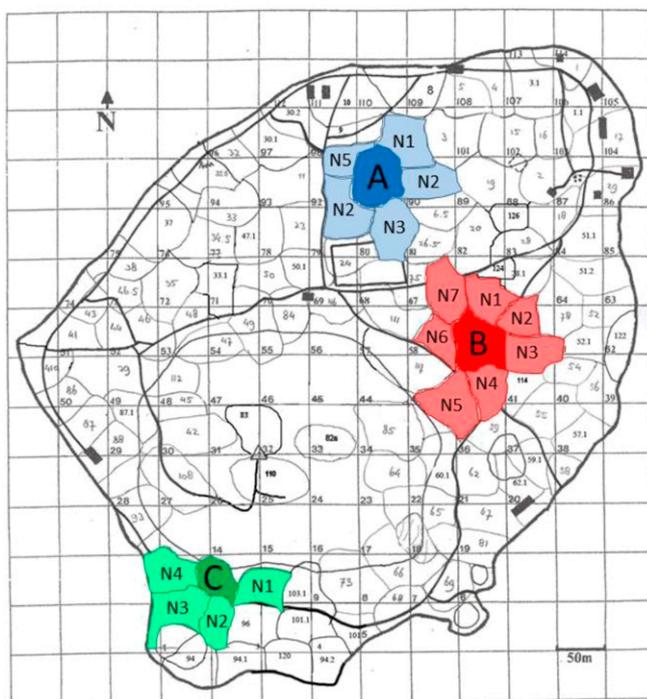
interact are missing. Second, it is unclear whether the influences of kinship and familiarity depend on other aspects of the social environment, such as the intensity of conflicts and level of local competition. Third, while there is some evidence that the degree of territorial conflict is linked to reproductive success (15), remarkably little is known about the mechanisms behind these patterns or the actual physiological cost of territoriality more generally. Fitness-linked markers of individual physiological condition give researchers the opportunity to link levels of territorial conflict with energy expenditure and somatic indicators of cost, thus shedding light on the overall benefit that conflict resolution between neighbors has for individual fitness.

Here, we investigate how kinship and familiarity act and interact with each other as well as with the broader social environment to influence the immediate and long-term physiological costs of territorial conflict in the cooperatively breeding Seychelles warbler *Acrocephalus sechellensis*. In this species, dominant breeding pairs (accompanied by up to five subordinate individuals) occupy stable year-round territories that the pair vigorously defends against conspecific intruders (19, 20). Both males and female breeders contribute to, and are equally likely to initiate, territorial defense (21), while subordinates usually do not chase intruders or monitor territory borders (22). Breeding pairs are socially monogamous and tend to remain together on the same territory for life but also engage in extrapair copulations resulting in high levels (*ca.* 40%) of extrapair paternity (23, 24), the majority of which is gained by breeding males living in nearby territories (24). The relatively long lifespan of this species (mean, 5 y) (25) and the stability of territories in space and time (19) mean that dominant territory owners usually occupy a territory for several consecutive years and hence repeatedly interact with the same neighbors. However, breeder displacement (26) or death and the occasional appearance and disappearance of territories also create temporal variation in the social neighborhood. This variation allows us to examine longitudinal changes in individual physiological condition in response to changing levels of conflict over territory boundaries.

We first quantify variation in conflict at territory boundaries by investigating the occurrence of physical fights between focal individuals and their neighbors in relation to kinship and familiarity. Previous work has shown intraspecific aggression at boundaries to be an important component of territorial behavior in this species (20–22). We then test whether and how properties of the social neighborhood (depicted in Fig. 1), including neighbor density, genetic relatedness, and social familiarity, interact to influence three fitness-related components of physiological cost in focal individuals. (i) We measure the change in body mass between two sampling points ( $\Delta$ Mass) as a function of change in the social neighborhood between the same two points. The use of body mass as a linear measure of physiological condition can be problematic in species where flight maneuverability is linked to predation risk (27, but see also ref. 28). However, adult Seychelles warblers have no predators (29), and body mass has been linked to various other components of physiological condition (30, 31), suggesting that this measure is a useful indicator of current territorial costs. (ii) We measure the change in telomere length ( $\Delta$ RTL) in focal individuals as a function of mean social neighborhood properties over the sampling period. Telomere length is a widely used bioindicator of somatic stress (32) that predicts survival in the Seychelles warbler (33, 34) and has also been shown to reflect the accumulation of somatic damage (35) arising through heightened metabolic costs and oxidative stress (36). (iii) We evaluated short-term survival prospects in relation to mean neighborhood properties over the sampling period. We determined whether each focal bird was still alive in the year following the final time it was caught and sampled.

## Results

**Physical Aggression Between Neighbors.** Focal males were significantly more likely to fight at borders where they were less related



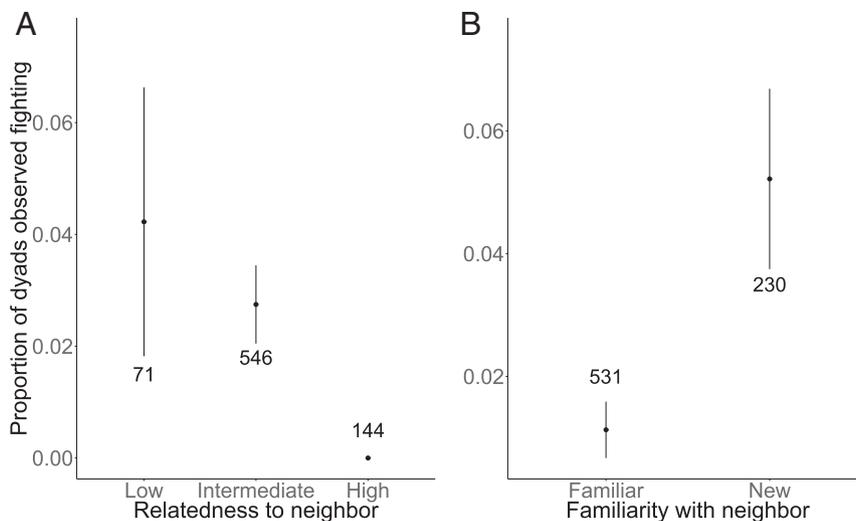
**Fig. 1.** Example of a spatial territory map of the Seychelles warbler population on Cousin Island during the 2006 main season, showing the distribution of territories across the island and the method by which a social neighborhood was defined. In this example, three focal individuals, A, B, and C (highlighted in blue, red, and green, respectively), were sampled in their respective territories. The territories that border the focal territory make up that individual's social neighborhood in the given season.

to the male neighbor (Fig. 2*A* and Table 1) or where the male neighbor was new in the neighborhood (Fig. 2*B* and Table 1). The likelihood of focal males fighting at boundaries was not related to relatedness or familiarity between the focal male and neighboring females (Table 1). Focal-female fights did not vary with the relatedness or familiarity of their neighbors of either sex (Table 1).

**Immediate Influences of the Social Neighborhood: Body Mass.** Among males who experienced an increase in neighbor density, those who became more related to their male neighbors gained more body mass than those that became less related (Fig. 3*A* and *C* and Table 2). Males who experienced an increase in the number of new neighbors (i.e., neighbor familiarity decreased) lost more mass, but again only when total neighbor density increased (Fig. 3*B* and *D* and Table 2). The top model set for focal-male  $\Delta$ Mass also contained changes in all five properties of the social neighborhood as main effects, but none apart from neighbor density were significant predictors of  $\Delta$ Mass (Table 2). Change in group size was not present in the top model set.

Focal-female  $\Delta$ Mass did not vary with changes in any of the social neighborhood properties or group size. The top model set contained a single predictor, change in neighbor density, but this was not significant (Table 3).

**Long-Term Influences of the Social Neighborhood: Telomere Dynamics and Survival.** Among focal males living at high neighbor densities, relatedness to male neighbors was positively related to  $\Delta$ RTL (Table 2), but this was not the case for males living at medium and low neighbor densities (Fig. 4). The relationship between new male neighbors and focal-male  $\Delta$ RTL varied with relatedness to those neighbors (Table 2): Males who experienced a higher



**Fig. 2.** Territorial fights involving focal male Seychelles warblers in relation to kinship and familiarity among neighbors ( $n = 761$  focal–neighbor dyads). (A) Focal males were more likely to be observed fighting male neighbors of lower relatedness (modeled as a continuous variable but factorized here for clarity). Males were never seen fighting neighbors of high ( $R > 0.25$ ) relatedness. (B) Focal males were more often observed fighting unfamiliar than familiar male neighbors. Dots and bars represent proportion of birds observed fighting, error bars represent the SE, and sample sizes denote the number of focal–neighbor dyads per group.

number of new male neighbors lost more telomere repeats, but mainly when relatedness to those neighbors was low (Fig. 5). Individuals who lived in smaller groups across the sampling period experienced more telomere shortening, and the degree of telomere shortening also increased with the amount of time between first and last sampling (Table 2). The top model set also contained all five properties of the social neighborhood, age at first sampling, and territory quality as main effects, but none of these was a significant predictor of  $\Delta$ RTL (Table 2).

$\Delta$ RTL of focal females was not related to any properties of the social neighborhood. The top model set included time between first and final sampling, neighbor density, number of new male and female neighbors, relatedness to female neighbors, mean territory quality, and mean group size, but none of these predictors was significant (Table 3). Relatedness to male neighbors and all interaction terms were absent from the top model set.

In the year directly following the final sampling, 40% of males and 24% of focal females in our dataset had died. However, neither focal male nor focal female survival was predicted by any of the social neighborhood properties across the sampling period. In focal males, age at first sampling, relatedness to male neighbors, number of new male neighbors, and mean group size were present in the top model set but were not significant (Table 2). In focal females, the number of new male neighbors, neighbor density, relatedness to male neighbors, and mean group size were in the top model set but again were not significant (Table 3).

## Discussion

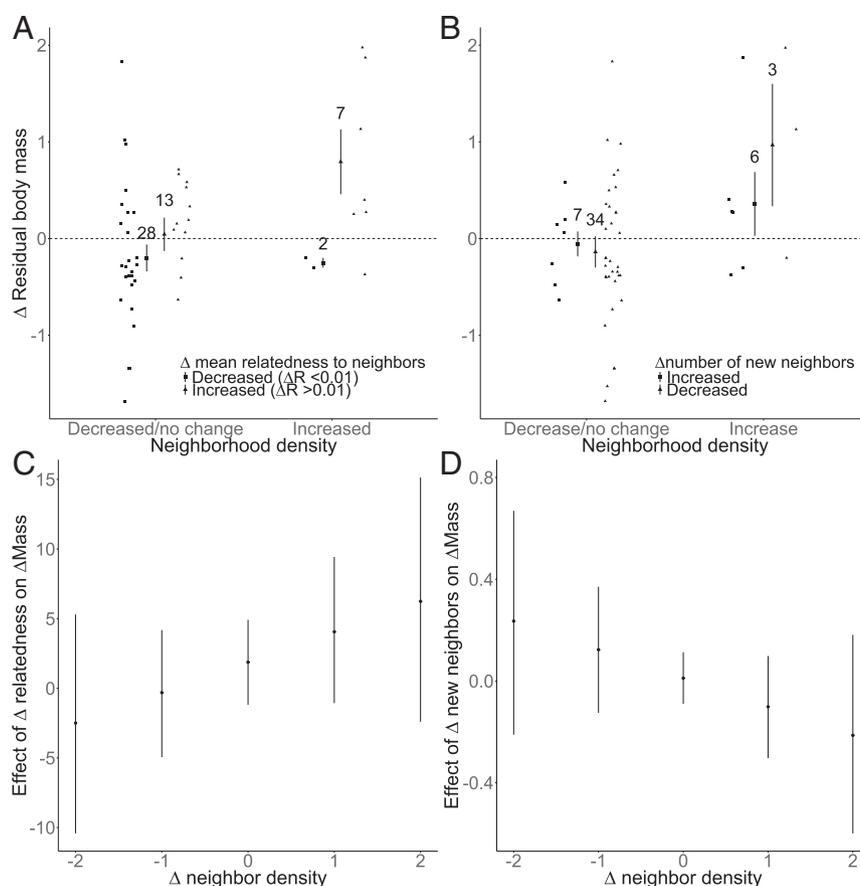
Territory boundaries represent an agreement over the division of space but, depending on the degree of conflict between neighbors, can be costly to maintain. In the Seychelles warbler, male territory owners are more often observed fighting at borders shared with unrelated and/or unfamiliar male neighbors. In line with this, males appear to gain an immediate benefit (in terms of increased body mass) from becoming more related to or familiar with male neighbors, but only when the total number of neighbors increases. Males also gain long-term benefits (in terms of reduced telomere loss) from having related male neighbors when living at high densities. Additionally, males lose more telomere repeats when living next to unfamiliar male neighbors, but only if these neighbors are not relatives. In contrast, focal females do not appear to respond to neighbor relatedness or familiarity with respect to territorial conflict or the associated physiological costs, suggesting that the social neighborhood is less important for females than for males. Our findings provide evidence for a complex interplay between kinship, familiarity, sex, and other aspects of the social environment that determines the cost of territorial conflict in wild animals. We discuss these results and their implications below.

**Physical Aggression Between Neighbors.** Males were more likely to be observed fighting male neighbors that they were less related to or that were new in the social neighborhood (Fig. 2). The frequency of observed fights was very low: out of a total 1,333 focal–neighbor

**Table 1.** The influence of neighbor relatedness and familiarity on the likelihood of focal-male and -female Seychelles warblers being observed fighting at a territory boundary

Sex	Predictor	Estimate $\pm$ SE	RI	P
Male ( $n = 761$ focal–boundary dyads)	<b>Relatedness to male neighbor</b>	<b><math>-2.38 \pm 1.24</math></b>	<b>1.00</b>	<b>0.05</b>
	<b>New male neighbor (vs. familiar)</b>	<b><math>1.68 \pm 0.62</math></b>	<b>0.63</b>	<b>&lt;0.01</b>
	Relatedness to female neighbor	$0.93 \pm 0.70$	0.30	0.18
	New female neighbor (vs. familiar)	$-0.46 \pm 0.67$	0.15	0.49
Female ( $n = 572$ focal–boundary dyads)	New female neighbor (vs. familiar)	$-1.89 \pm 1.05$	1.00	0.07
	Relatedness to male neighbor	$0.27 \pm 0.56$	0.19	0.63
	Relatedness to female neighbor	$-0.11 \pm 0.54$	0.17	0.84
	New male neighbor (vs. familiar)	$0.13 \pm 0.67$	0.17	0.85

Significant predictors are in boldface type. RI, relative importance.



**Fig. 3.** Interacting effects of relatedness, familiarity, and neighbor density on  $\Delta$ Mass of focal-male Seychelles warblers ( $n = 50$ ). (*A* and *B*)  $\Delta$ Mass is more positive when focal males become more related to (*A*) or familiar with (*B*) their male neighbors, but in both cases only when neighbor density also increases. Relationships were modeled as continuous variables but are factorized for visual clarity. Large dots and error bars represent means and SEs, small dots represent raw data, and sample sizes per group are denoted above each bar. (*C* and *D*) The same information is displayed using continuous data. When neighbor density increases, the conditional effect of male relatedness on  $\Delta$ Mass (y axis) becomes more positive (*C*), and the effect of new male neighbors on  $\Delta$ Mass (y axis) becomes more negative (*D*).

dyads (in which each dyad consists of a focal individual and one of its neighbors), we recorded fights in 32 (2.5%) of them. This suggests that, rather than providing a direct mechanism by which kinship and familiarity affect body mass and telomere loss, fighting is a relatively rare manifestation of ongoing, less visible conflict between unrelated and unfamiliar neighbors. Although this analysis consisted of fairly small sample sizes and should therefore be interpreted with caution, our results support those found in other species. For example, in willow ptarmigans (*Lagopus lagopus*) males were more likely to fight unfamiliar neighbors (16) and were less aggressive toward related neighbors (37), while several studies in salmonid fish demonstrate reduced aggression in kin shoals (38–40). It would be extremely interesting to investigate the exact function of kinship and familiarity in this context: Are fights less common between cooperating neighbors because each individual is less willing to “cheat” by crossing the agreed boundary or because cooperating neighbors do not enforce the boundary so strictly, leading to more territory overlap? Evidence from a handful of studies points to the latter, at least with respect to kinship between neighbors (13, 41, 42, reviewed in ref. 15), but it is currently unclear whether territory overlap (accepted cheating) or reduced incentive to trespass (assured cooperation) also occurs between familiar neighbors.

**Immediate Benefits of Neighbor Kinship and Familiarity.** Given that body mass reflects an individual’s physiological state in the Seychelles warbler (30), as is broadly assumed across many species (43, but

see ref. 44 for limitations of this metric), individuals who spend more time finding food and/or less energy on territorial defense should have greater mass. In high-density areas, we found that males who were more related to or familiar with their male neighbors in the later of two sampling points were also heavier at the second sampling point (Fig. 3). Although drawn from small sample sizes (only nine focal males experienced an increase in neighbor density in this analysis), these patterns suggest a within-individual response to changes in levels of territory boundary conflict. Somewhat similar results have been reported in zebrafish *Danio rerio*, in which juveniles grew to a greater size when shoaling with familiar kin than with unfamiliar nonkin (45). In the current study, both familiarity and relatedness appear to play independent roles in mitigating territorial costs. However, both these relationships were present only when focal males had a high number of neighbors; this result is intuitive under the assumption that territorial costs, and hence the degree to which kinship and familiarity can be influential, accumulate with the number of boundaries to maintain.

Since body mass changes on a very short temporal timescale (46), one assumption of using  $\Delta$ Mass to measure changing territorial conflict is that the level of social conflict with neighbors remains relatively equal across the season in which an individual is sampled. If conflict between neighbors reduces within a season, the relationship between body mass and territorial conflict (i.e., relatedness to and familiarity with neighbors) will become weaker over the season. We have two reasons to suspect that this is not the case in the Seychelles warbler. First, observations in the field

**Table 2. Model-averaged estimates and relative importance (RI) of social neighborhood properties in relation to  $\Delta$ Mass,  $\Delta$ RTL, and survival of focal-male Seychelles warblers**

Response	Predictor	Estimate $\pm$ SE	RI	P
$\Delta$ Mass ( $n = 50$ , eight models in top set)	<b>Change in relatedness to male neighbors <math>\times</math> change in neighbor density</b>	<b>0.95 <math>\pm</math> 0.40</b>	<b>0.12</b>	<b>0.02</b>
	<b>Change in number of new male neighbors <math>\times</math> change in neighbor density</b>	<b>-1.40 <math>\pm</math> 0.63</b>	<b>0.12</b>	<b>0.03</b>
	<b>Change in neighbor density</b>	<b>0.47 <math>\pm</math> 0.22</b>	<b>0.90</b>	<b>0.04</b>
	Change in number of new male neighbors	-0.68 $\pm$ 0.35	0.45	0.06
	Change in number of new female neighbors	0.69 $\pm$ 0.39	0.56	0.08
	Change in relatedness to male neighbors	0.40 $\pm$ 0.23	0.47	0.09
$\Delta$ RTL ( $n = 52$ , 10 models in top set)	Change in relatedness to female neighbors	-0.23 $\pm$ 0.21	0.10	0.30
	<b>Group size</b>	<b>0.33 <math>\pm</math> 0.12</b>	<b>1.00</b>	<b>0.01</b>
	<b>Relatedness to male neighbors <math>\times</math> neighbor density</b>	<b>0.62 <math>\pm</math> 0.25</b>	<b>0.19</b>	<b>0.01</b>
	<b>Relatedness to male neighbors <math>\times</math> number of new male neighbors</b>	<b>0.39 <math>\pm</math> 0.18</b>	<b>0.21</b>	<b>0.03</b>
	<b>Time between samples</b>	<b>-0.28 <math>\pm</math> 0.14</b>	<b>0.71</b>	<b>0.05</b>
	Number of new male neighbors	-0.16 $\pm$ 0.16	0.46	0.31
	Relatedness to male neighbors	-0.14 $\pm$ 0.14	0.40	0.32
	Relatedness to female neighbors	0.11 $\pm$ 0.12	0.09	0.36
	Age at first sampling	-0.10 $\pm$ 0.12	0.08	0.40
	Territory quality	-0.09 $\pm$ 0.13	0.07	0.51
	Neighbor density	<0.01 $\pm$ 0.13	0.19	0.98
Survival ( $n = 58$ , five models in top set)	Age at first sampling	-0.76 $\pm$ 0.55	0.29	0.18
	Relatedness to male neighbors	-0.33 $\pm$ 0.55	0.13	0.56
	Number of new male neighbors	0.33 $\pm$ 0.56	0.13	0.57
	Mean group size	0.24 $\pm$ 0.55	0.12	0.68

Significant predictors are in boldface type. Variables not included in the top model set are not reported. Sample sizes vary, as not all measured variables were available for all individuals and are therefore given separately for each model.

suggest that territorial interactions, such as those arising when a new territory is established, continue throughout the season and often into the following season. Second, our analyses of neighbor familiarity show that new neighbors are more costly (in terms of mass and telomere loss) than neighbors that were familiar from the previous season. If conflict between neighbors diminishes within the course of a single season, we would be unlikely to detect this difference. Nonetheless, the temporal component of conflict resolution is likely to be very important in understanding social interactions more generally (47); it would be extremely interesting to test for fine-scale variation in the duration of conflict resolution between social partners of different relatedness and familiarity.

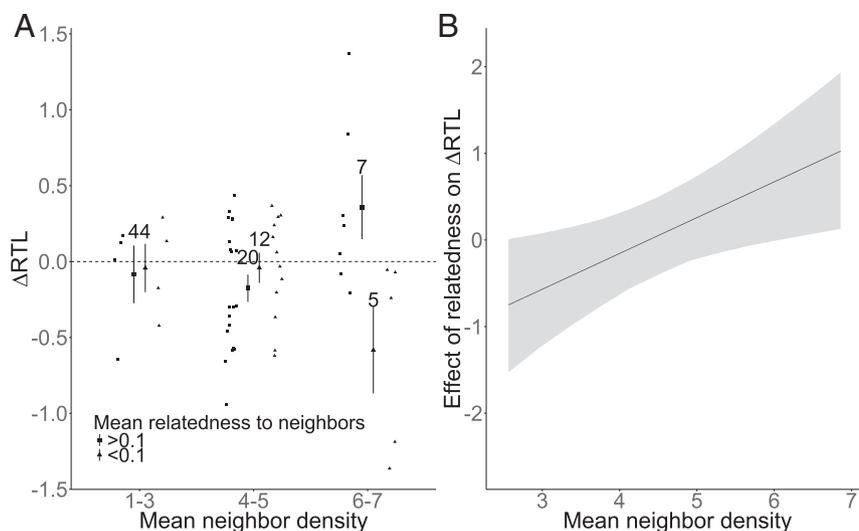
**Long-Term Benefits of Neighbor Kinship and Familiarity.** Telomere shortening is exacerbated by the damaging effect of oxidants that arise in the body as a result of metabolic processes and other factors (36). In wild animals, more rapid telomere shortening can

arise through poor internal state (e.g., refs. 33 and 48) or sub-optimal environmental conditions (e.g., refs. 49 and 50) and is known to predict survival in the Seychelles warbler (33, 34) and other species (51). We found that focal males experienced less telomere attrition when they were more related to their male neighbors, but only when they had many neighbors (Fig. 4). We suggest that exacerbated telomere shortening results from the physiological stress of continued conflict with neighbors, which reduces the amount of time and resources that can be spent creating antioxidant defenses and maintaining somatic condition more generally. Males who are in greater conflict with neighbors over territory boundaries must spend more time patrolling borders, singing, and engaging in physical competition; it seems logical that the degree to which these costly activities hinder somatic maintenance depends on the number of borders to maintain. In the same way that body mass appears to reflect variation in territorial conflict in the immediate term, telomere dynamics appear

**Table 3. Model-averaged estimates and relative importance (RI) of social neighborhood properties in relation to  $\Delta$ Mass,  $\Delta$ RTL, and survival in focal-female Seychelles warblers**

Response	Predictor	Estimate $\pm$ SE	RI	P
$\Delta$ Mass ( $n = 31$ , two models in top set)	Change in neighbor density	0.46 $\pm$ 0.35	0.35	0.22
	Intercept	-0.09 $\pm$ 0.28	1.00	0.75
$\Delta$ RTL ( $n = 32$ , 13 models in top set)	Time between samples	-0.30 $\pm$ 0.17	0.51	0.09
	Number of new female neighbors	-0.24 $\pm$ 0.17	0.19	0.18
	Neighbor density	-0.23 $\pm$ 0.17	0.29	0.20
	Group size	-0.22 $\pm$ 0.17	0.09	0.21
	Territory quality	0.20 $\pm$ 0.17	0.24	0.26
	Number of new male neighbors	-0.20 $\pm$ 0.17	0.06	0.26
Survival to next year ( $n = 38$ , five models in top set)	Relatedness to female neighbors	-0.15 $\pm$ 0.17	0.05	0.41
	Neighbor density	0.80 $\pm$ 0.84	0.19	0.36
	Number of new male neighbors	0.65 $\pm$ 0.89	0.16	0.49
	Relatedness to male neighbors	-0.55 $\pm$ 0.77	0.15	0.49
	Mean group size	0.42 $\pm$ 0.82	0.14	0.62

Variables not included in the top model set are not reported. Sample sizes vary, as not all measured variables were available for all individuals and are therefore given separately for each model.



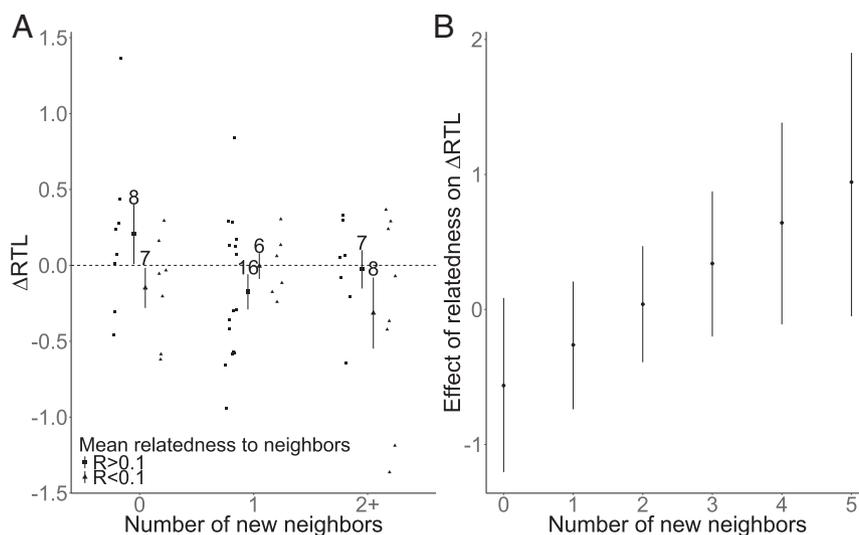
**Fig. 4.** Interacting effects of relatedness to male neighbors and neighbor density on  $\Delta$ RTL in focal-male Seychelles warblers ( $n = 52$ ). (A)  $\Delta$ RTL is more positive when relatedness to male neighbors is high, but only at high neighbor density. Relationships were modeled as continuous variables but are factorized for visual clarity. Large dots and error bars represent means and SEs, small dots represent raw data, and sample sizes per group are denoted above each bar. (B) The conditional effect of relatedness on  $\Delta$ RTL ( $y$  axis) becomes more positive as mean neighbor density increases.

to reflect longer-term somatic damage. Perhaps more intriguing is the finding that neighbor familiarity had different influences on telomere dynamics according to the focal male's relatedness to his neighbors (Fig. 5). High numbers of new male neighbors were associated with greater telomere shortening, but high neighbor relatedness appeared to mitigate that relationship. This complex interaction between relatedness and familiarity illustrates the difficulty in separating kin-selected and non-kin-selected pathways to cooperation: Depending on the relative strength of each mechanism, one may obscure the other.

Each new neighbor has a unique set of spatial demands depending on its resource requirements, competitive ability, and personality traits, and these require potentially costly renegotiation of the territory boundary (10). If the new neighbor is a relative, negotiation costs may be less severe, as the neighbor's interests are likely

to be more aligned with those of the focal individual. If not, the focal individual will benefit most by keeping that neighbor for as long as possible to avoid constant renegotiation (which is potentially harmful and costly) with new neighbors. Selection for maintenance of relationships with familiar competitors is known more formally as the dear enemy phenomenon (9). With regard to the current study, we suggest that dear enemy-type interactions are responsible for the observed relationships between neighbor familiarity and both body mass and telomere dynamics.

Despite evidence that properties of the social neighborhood are related to both body mass and telomere dynamics, we found no relationship between any neighborhood properties and the short-term survival of either focal males or focal females. This is perhaps not surprising, given the stochasticity and potential confounds inherent in survival measures (52) and the fact that our relatively



**Fig. 5.** Interacting effects of relatedness and familiarity on focal-male  $\Delta$ RTL in Seychelles warblers ( $n = 52$ ). (A)  $\Delta$ RTL is more negative when the number of new male neighbors increases, but only when relatedness to those neighbors is low. Relationships were modeled as continuous variables but are factorized for visual clarity. Large dots and error bars represent means and SEs, small dots represent raw data, and sample sizes per group are denoted above each bar. (B) The conditional effect of relatedness on  $\Delta$ RTL ( $y$  axis) becomes more positive as the number of new neighbors increases.

small sample size may be sufficient to detect only very strong survival differences. It is also possible that a relationship between territorial cooperation and survival would manifest over longer timespans. In this study we considered the effect of the social neighborhood on survival over a specific period of an individual's life, but survival-based consequences of heightened territorial conflict may manifest over entire lifetimes. Given the established association between telomere length and survival in the Seychelles warbler (34), it can nonetheless be reasonably concluded that the observed physiological stress associated with heightened territorial conflict detrimentally impacts individual fitness.

**Genetic and Social Relatedness Measures.** Evidence to date suggests that kin discrimination in birds is based on indirect cues of relatedness, such as matching phenotype (e.g., recognizing similarity in song) or spatial location (e.g., assuming individuals in a natal territory are kin) (53). Unfortunately, we were unable to accurately assess social relatedness in the current dataset; we therefore used genetic pairwise relatedness to infer kinship between focal individuals and their neighbors. However, high levels of extrapair paternity in this species (*ca.* 40%) (54) lessen the extent to which genetic relatedness matches social relatedness. This raises the question of why we found that genetic relatedness between neighbors affects not only their propensity to fight but also the degree to which they benefit from each other. We envisage two possible reasons: (i) Seychelles warblers use indirect phenotypic and spatial cues to discriminate kin, but the effect of perceived (social) relatedness on territorial costs is so strong that we were still able to detect it using genetic relatedness; or (ii) Seychelles warblers use genetic cues to determine kinship and are responding directly to genetic relatedness. Previous work in the Seychelles warbler suggests that relatedness is estimated using association cues (55, 56), suggesting that the former possibility is more likely. However, there is some evidence in other bird species for direct use of allelic similarities to discriminate kin, especially in regard to odor recognition (57, 58). It would be extremely interesting to repeat the analyses we describe here with measures of social relatedness in both this and other social species.

**Sex Differences in Costs of Territoriality.** In all components of our investigation, we found evidence that territorial costs are mediated by kinship and familiarity for males but not for females. Focal female body mass and telomere length did not vary with any properties of the social environment, and females did not appear to fight more with certain types of neighbor (although the small sample size admittedly limits our interpretation of this result). In addition, focal male territoriality costs appear to be much less dictated by the identity of female neighbors than that of male neighbors. Interestingly, our finding that only males seem to respond to the social environment fits with the pattern of female-biased dispersal distance previously reported in the Seychelles warbler (21, 59); perhaps selection favors reduced dispersal distance in males to promote kinship and familiarity with neighbors.

**Spatial Confounds in Social Neighborhoods.** Because kin- and, to some extent, familiarity-based neighborhoods form as a result of short-distance dispersal (11), an alternative explanation for our results is that individual differences in dispersal strategy drive both the formation of social neighborhoods and variation in physiological costs. One such confound could manifest through variation in territory quality: If individuals from high-quality territories are selected to disperse shorter distances (and remain in a high-quality area of the population), high neighbor relatedness may be linked to measurements of physiological cost in the absence of a causal relationship. While important to consider, we suspect that this is not the case in our population for three reasons. First, remaining in a high-quality area should be equally as important for females

as for males, but our results show that only focal males benefit from living in areas of high neighbor relatedness and familiarity. Second, our analysis of longitudinal  $\Delta$ Mass shows that focal males gain mass when they become more related to male neighbors, suggesting that changes in relatedness, rather than initial individual quality, drive this relationship. Last, if high territory quality drives short-distance dispersal, we would expect a consistent presence of strong kin neighborhoods in high-quality areas of the island, but Fig. S1 suggests that the occurrence of high neighbor relatedness actually varied spatially across the years of our study. Taken together, these arguments suggest that differences in territorial costs as a result of relatedness and familiarity between neighbors, rather than viscosity among high-quality individuals, explain the results we present here.

However, spatial confounds could also manifest through other pathways, such as inbreeding depression. Inbreeding influences the evolution of dispersal strategies in many species (60) and has been shown to reduce the telomere length (35) and reproductive success (61) of Seychelles warblers. However, there is no evidence of inbreeding avoidance with respect to partner choice in this species (62), and recent work demonstrated that dispersal distance is not driven by inbreeding avoidance (21); together, these suggest that individuals with more-related neighbors may actually be more inbred (and hence lower in quality). Since the potential confound of inbreeding is predicted to drive a relationship in the opposite way to our hypothesis (specifically, individuals in strong kin-based neighborhoods may be more inbred and hence lower, rather than higher, in quality), we find it unlikely to explain our results.

## Conclusions

The degree to which kin selection and mutualistic benefits can resolve conflicts between interacting animals remains one of the most intriguing puzzles in evolutionary biology. In Seychelles warblers, we show that not only it is possible for both these pathways to reduce the costs of conflict over space but also that they can interact with each other and with the social environment to differentially affect costs of territoriality. We also provide evidence that the benefits of peaceful boundaries are related to the rate at which an individual accumulates physiological damage (as measured through telomere attrition), suggesting that interactions between neighbors have the potential to significantly affect fitness and population structure. Our results also highlight the importance of sex differences in determining how mitigating conflict can be beneficial and suggest a complex interplay between kinship and familiarity that can help explain the causes and consequences of behavioral conflict more generally.

## Methods

**Field Data.** We collected data from the population of *ca.* 250 adult Seychelles warblers living on *ca.* 110 territories on Cousin Island, Seychelles, which has been subject to intensive individual-level monitoring since 1997 (54). In this period the population has been the source of two conservation-based translocations to other islands [in 2004 (63) and 2011 (64)]. To exclude potential disruption of the population density and resource availability after these translocations, here we focus exclusively on the period between 2006 and 2010, during which time there was no translocation-related disturbance to the population. Across the 5 y of the study, fieldwork was conducted during the main breeding season (June–September) and, in some years, during the minor breeding season (January–March). Each season, as many birds as possible were caught using mist nets and, if not already ringed, were given a unique British Trust for Ornithology metal ring and three-color rings for individual identification. A *ca.* 25- $\mu$ L blood sample was taken at each catch. Body mass (to 0.1 g), tarsus length (to 0.1 mm), and time of catch (early: 06:30–11:00 h; midday: 11:00–15:00 h; or late: 15:00–18:00 h) were also recorded and used to calculate residual body mass, which we used in analyses of immediate physiological condition (see below). This sampling regime is identical to that used in previous years, meaning that *ca.* 96% of birds in the population were already ringed and genotyped at the start of this study (24, 25).

Our dataset contained longitudinal samples from 58 focal breeding males and 38 focal breeding females (herein, “focal males” and “focal females,” respectively) that were initially caught (within this study period) between 2006 and 2008, with at least one repeat catch by 2010. We monitored the presence of each focal individual in the population after their final catch. Since dispersal from the island is virtually absent (65), and resighting probability is extremely high, focal individuals could be confidently assumed to be dead if they were not seen for two successive main breeding seasons after their final catch (34, 66).

In every main breeding season, each territory was surveyed to determine the identity of the dominant breeding pair (easily recognized through courtship and pair behavior) and the presence of any subordinate birds living in the territory (19). We distinguished between males and females based on molecular sexing (see below). Groups forage exclusively within their own territory and defend territory boundaries from conspecifics, so we could accurately identify these boundaries based on behavioral observations (19, 20). During surveys of territory boundaries and group composition, we also opportunistically observed physical fights at boundaries. Fights are extremely fast and hard to follow, but, where possible, we recorded the identity of the birds involved in the fight and the boundary at which the fight occurred. This yielded a total of 35 observations of fighting between a focal individual and identified neighbors. Under this sampling regime, the likelihood of observing a fight increases with the amount of time spent surveying a territory, but surveying effort was relatively equal across territories, so we do not expect this to bias our analysis. Seychelles warblers are insectivorous, and territory quality in each main breeding season was measured as insect density per unit of foliage in each territory, following Brouwer et al. (66). In each main season, we produced a map specifying each territory’s location (Fig. 1), drawn based on a grid system of static poles that cover the island at 50-m intervals (59) and georeferenced in ArcMap 10.3 (ESRI, <https://esri.com>). Spatial and territorial data were collected only in the main seasons due to a lack of resolution in the (relatively brief) minor seasons, but, since territories are relatively stable (19), data collected in the main breeding season are likely to be a good representation of the year-round territorial environment.

**Molecular Data.** DNA was extracted from blood samples with a Qiagen DNeasy Blood and Tissue Kit and was used to determine sex following Griffiths et al. (67) and individual genotypes at a panel of 30 microsatellite markers already developed for the Seychelles warbler (62, 68). We compared the suitability of two pairwise relatedness estimators, Queller and Goodnight (QG) (69) and Lynch and Ritland (LR) (70), in the R package related (71) and determined that QG was more suitable in our microsatellite panel (Fig. S2 and Table S1). QG relatedness estimates between all dominant breeders in the population over the study period (including all focal individuals and all neighboring breeders) were calculated in GenAlEx 6 (72). Pairwise relatedness has previously been shown to reflect pedigree relatedness in the Seychelles warbler (62), and heterozygosity across our microsatellite panel is also known to reflect genome-wide heterozygosity (31).

We measured telomere length in each blood sample according to the protocol described in detail elsewhere (33–35). Briefly, we calculated a relative measure of telomere length as the concentration of telomeric DNA relative to that of a normalizer gene, *GAPDH*, using quantitative real-time PCR. We then calculated each individual’s  $\Delta$ RTL over the sampling period as the difference between telomere length at first and final sampling, such that positive values indicate increases in telomere length and negative values indicate decreases in telomere length.

**Defining Neighborhood Properties.** We used the territory map produced in each main season to define a focal individual’s “social neighborhood,” which consisted of the dominant breeding male and female owners (henceforth “male neighbors” and “female neighbors”) of all territories that directly bordered part of the focal individual’s territory (Fig. 1). We then calculated five parameters of the social neighborhood. The first parameter, neighbor density, was associated with the expected intensity of territorial interactions and was calculated as the number of territories in the social neighborhood (which is unrelated to territory size; see Fig. S3). The second and third parameters, relatedness to male neighbors and relatedness to female neighbors, were associated with kinship and were calculated as the mean pairwise genetic relatedness between the focal individual and all other dominant males and females, respectively, in the neighborhood. The final two parameters, number of new male neighbors and number of new female neighbors, were associated with familiarity and were calculated as the number of male and female neighbors, respectively, that did not occupy the dominant position in their territory in the previous year and hence were new

in the focal individual’s social neighborhood. If the focal bird itself was newly dominant in that year, we considered all its neighbors to be new. We calculated these five variables separately for each main season but also calculated the mean male and female relatedness values and total number of new male and female neighbors across the longitudinal sampling period for each focal individual.

**Statistical Analyses.** We used a model-averaging approach to determine which properties of the social neighborhood influenced the likelihood of territorial fights, residual body mass, telomere dynamics, and survival. Exploring the relative influence of kinship and familiarity on territorial costs under varying social circumstances requires testing interactions between different neighborhood properties. To investigate whether such interactions are equally important for male and female territory owners while simultaneously avoiding the need to model numerous complex, three-way interactions, we created separate models for focal males and females throughout. Collinearity between all variables was checked before modeling using variance inflation factors (VIF). In no case was the VIF large enough to cause issues in the analysis (all VIF <4) (73). Using the package MuMIn (74) in R (version 3.3.1) (75), we created a global mixed-model that contained all variables, plus selected interactions of interest, as standardized predictors so that both main effects and interactions could be interpreted (76). We report natural averages of each parameter across the top model set, which contained all models in which the change in Akaike’s second-order information criterion ( $\Delta$ AICc) was  $\leq 2$  (77). Natural averaging can inflate effect sizes and *P* values but is well suited to determining the effect of a given variable when the additional variance explained by that parameter is likely to be small (78, 79), as is the case with biological markers such as body mass and telomere dynamics. Complete outputs for top model sets are presented in Table S2. Since our global models contain a large number of parameters relative to the sample size (which increases the risk of over-fitting and the production of spurious results) (77, 79), we repeated our analyses using reduced models that contained only parameters that were deemed important ( $P < 0.1$ ) in the full analysis. The results of this second analysis were qualitatively identical to those we report and can be found in Table S3.

We first tested whether focal individuals were more likely to engage in territorial fights with unrelated or unfamiliar neighbors by considering each focal–neighbor dyad (consisting of a focal individual and one of its neighbors) in our dataset as an individual data point at which a territorial fight has the potential to occur. Separately for focal males and females, we tested whether fight occurrence for a given focal–neighbor dyad (whether we observed a fight at the boundary or not in a given season; binomial response) was predicted by relatedness to and familiarity with the male and female neighboring territory owners. We included two random effects: focal individual identity, to account for repeat sampling of focal individuals across the years of the study, and neighboring territory identity, to account for similarity in neighbor identity between focal individuals in the same area of the island.

To measure the immediate influence of the social neighborhood on individual costs, we tested whether the  $\Delta$ Mass between two sampling points was related to the corresponding change in each of the five social neighborhood properties (modeled as continuous variables) as measured at the same two sampling points. To determine whether the influence of kinship and familiarity depends on the intensity of territorial interactions, we also tested whether the change in these components interacted with the change in neighbor density between the two sampling points (change in relatedness or change in number of new neighbors  $\times$  change in neighbor density). To investigate the interplay between kinship and familiarity, we tested whether change in the number of new neighbors had a varying effect on  $\Delta$ Mass according to the change in relatedness (change in relatedness  $\times$  change in number of new neighbors, separately for male and female neighbors). We also included change in group size between the two sampling points to account for between-sample variation in per-capita territorial resources (66). In addition, we included random effects of age at first sampling and time between the two samples. In males, we also included individual identity as a random effect, as some males had multiple measurements of  $\Delta$ Mass.

To measure the long-term influence of the social neighborhood on individual costs, we tested whether (i)  $\Delta$ RTL and (ii) survival to the year following the final sample (binomial response) were related to the mean of each of the five social neighborhood properties across the sampling period. We included interactions between neighbor density and each of the other social neighborhood properties and also tested whether the number of new neighbors had a differential effect on  $\Delta$ RTL and survival depending on mean neighbor relatedness (mean relatedness  $\times$  number of new neighbors, separately for male and female neighbors). We included three covariates: (i) the

focal individual's mean territory quality [accounting for environmentally induced differences in physiological costs (33)], (ii) mean group size [the number of independent resident birds in the territory, accounting for variation in per-capita territorial resources (66)] across the sampling period, and (iii) age at first sampling to account for age-related differences in telomere dynamics (34). In the analysis of  $\Delta$ RTL we also included the time (in years) between first and last sampling.

The spatial nature of our data posed a risk of nonindependence: If two focal individuals lived in adjacent territories, they would be included in each other's neighborhood and hence have the potential to influence each other. The correlation between neighborhood properties of neighboring focal individuals was consistently low (ca. 0.2) and therefore was unlikely to influence our results. However, there is also the potential for spatial autocorrelation between the social neighborhood and undetected environmental factors. We therefore tested whether similarity in individual body mass and telomere dynamics was related to the spatial proximity of two individuals. Using ArcMap 10.3, we calculated the center point of each territory using the spatial map of 2006 as a template and calculated the distance in meters between each of these center points. Using the *ncf* package in R, we calculated Moran's I (80) and the significance values of the residuals of regression models of each response variable

on all neighborhood properties. Moran's I was not significantly different from zero for the residuals of any of the predictor variables (Fig. S4), and a visual inspection of the distribution of neighborhood properties across the island did not reveal any spatial grouping of neighborhood relatedness, familiarity, or neighbor density (Fig. S1), so we conclude that spatial structure is unlikely to have influenced the results of our analyses.

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