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SOUTHWESTERN WILLOW FLYCATCHERS (*EMPIDONAX TRAILLII EXTIMUS*) IN A GRAZED LANDSCAPE: FACTORS INFLUENCING BROOD PARASITISM

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Abstract.—Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds") is an important factor contributing to the endangered status of the Southwestern Willow Flycatcher (*Empidonax traillii extimus*, hereafter "flycatcher"). We report on factors that influence brood parasitism on the flycatcher using seven seasons of nest data ($n = 491$ nests) collected in riparian patches comprising cottonwood (*Populus fremontii*), willow (*Salix* spp.), and boxelder (*Acer negundo*) along the Gila River in southwest New Mexico. We quantified habitat and landscape characteristics that might be associated with higher levels of parasitism and assessed the correlation between those and the observed incidence of nest parasitism. Given that cowbirds associate with cattle, we were particularly interested to determine whether the distance to active summer grazing would influence the frequency of brood parasitism. We found an apparent negative trend between the distance to grazing and brood parasitism, but this trend was not statistically significant. Rather, brood parasitism was more strongly correlated with characteristics of the habitat. Specifically, nests in larger patches, and nests built near the patch edge adjacent to the river, were more susceptible to parasitism, which suggests that these areas are preferred nesting habitat for cowbirds because of a potentially greater abundance of hosts. Parasitism was significantly lower within the core of large patches, but the insulating effect was not evident in small and medium-sized patches. Higher nest height was strongly correlated with lower probability of parasitism, most notably for nests in boxelders. Nests in boxelders were less susceptible to parasitism, whereas nests in willows were more susceptible to parasitism. We discuss the results in the context of other studies. We recommend that management efforts to recover the flycatcher should focus on increasing quality habitat, and we suggest that cattle management should focus on eliminating the adverse effects of grazing on riparian health as a more feasible option than removing cattle far enough from riparian corridors so as to preclude parasitism. *Received 27 January 2006, accepted 2 November 2006.*

Key words: brood parasitism, Brown-headed Cowbird, cattle grazing, *Empidonax traillii extimus*, endangered species, *Molothrus ater*, nesting ecology, riparian habitats, Southwestern Willow Flycatcher.

Empidonax traillii extimus en un Paisaje con Pastoreo: Factores que Influyen sobre el Parasitismo de la Nidada

Resumen.—El parasitismo de la nidada por parte de *Molothrus ater* es un factor importante que contribuye al estatus de especie en peligro de *Empidonax*

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traillii extimus. Presentamos información sobre los factores que influyen sobre el parasitismo de la nidada de *E. t. extimus* usando datos de nidos de siete estaciones (n = 491 nidos), colectados en parches ribereños de *Populus fremontii*, *Salix* spp. y *Acer negundo*, a lo largo del Río Gila en el sudoeste de Nuevo México. Cuantificamos las características del hábitat y del paisaje que podrían estar asociadas con niveles más alto de parasitismo y evaluamos la correlación entre éstos y la incidencia observada de parasitismo de nidos. Dado que *M. ater* se asocia con el ganado, estábamos particularmente interesados en determinar si la distancia a los sitios activos de pastoreo de verano influyen sobre la frecuencia de parasitismo de la nidada. Encontramos una tendencia aparentemente negativa entre la distancia a los sitios de pastoreo y el parasitismo de la nidada, pero esta tendencia no fue estadísticamente significativa. En lugar de esto, el parasitismo de nidada estuvo más fuertemente correlacionado con las características del hábitat. Específicamente, los nidos en los parches más grandes, y los nidos construidos cerca del borde de los parches adyacentes al río, fueron los más susceptibles al parasitismo. Esto sugiere que esas áreas podrían ser los ambientes preferidos de nidificación para *M. ater*, debido a una abundancia de hospederos potencialmente mayor. El parasitismo fue significativamente más bajo en el núcleo de los parches grandes, pero el efecto de asilamiento no fue evidente en los parches pequeños y medianos. La posición de los nidos a una altura mayor estuvo fuertemente correlacionada con una menor probabilidad de parasitismo, particularmente para los nidos en *A. negundo*. Los nidos en *A. negundo* fueron menos susceptibles al parasitismo, mientras que los nidos en las especies de *Salix* fueron más susceptibles al parasitismo. Discutimos nuestros resultados en el contexto de otros estudios. Recomendamos que los esfuerzos de manejo para la recuperación de *E. t. extimus* deberían enfocarse en incrementar la calidad del hábitat. También sugerimos que el manejo del ganado debería enfocarse en la eliminación de los efectos adversos del pastoreo sobre la condición de los ambientes ribereños, como una opción más realista que la remoción del ganado en las cercanías de los corredores ribereños como para evitar el parasitismo.

Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; hereafter "cowbirds") often has a negative effect on the nesting success of small passerines, and it is believed to be at least partly responsible for the decline of some sensitive bird species (Robinson et al. 1995). In the western United States, floodplains are especially suitable for cowbirds because of (1) foraging opportunities in a landscape dominated by agriculture and grazing and (2) breeding opportunities in riparian habitats, which support more bird species than any other habitat in the West (Knopf et al. 1988). Degradation of western riparian ecosystems is a conservation issue of great concern (Knopf et al. 1988), and habitat loss is a leading factor in the decline of some riparian-obligate breeding birds (Johnson 1989). The abundance of cowbirds in these ecosystems suggests that brood parasitism is an added threat for species that may already be experiencing declines.

The Southwestern Willow Flycatcher (*Empidonax traillii extimus*; hereafter "flycatcher") is an endangered subspecies and a riparian-obligate breeder (Sedgwick 2000, U.S. Fish and Wildlife Service [USFWS] 2002). Riparian ecosystems have been severely degraded by anthropogenic changes on floodplains and, as a result, the flycatcher has become extirpated from much of its former breeding range (USFWS 2002). The negative effect of brood parasitism by cowbirds on nest productivity is also listed as an important factor contributing to flycatcher population declines (Robinson et al. 1995, Whitfield and Sogge 1999, USFWS 2002). Despite the well-documented threat, reported proportions of parasitism on flycatcher nests are highly variable, and costs of parasitism on productivity and population viability remain unknown (Sedgwick 2000, Rothstein et al. 2003). It is known, however, that over the past century the cowbird population in the Southwest has grown and that brood parasitism on the flycatcher has correspondingly increased (Whitfield and Sogge 1999). Grazing on floodplains is common in the Southwest because the forage is generally better than in the adjacent uplands. With the associated threats of brood parasitism, proximity to grazing is, therefore, a serious concern in regard to flycatcher management.

In the arid West, floodplains are highly suitable for the cowbird during the breeding season. Agricultural landscapes are strong predictors of cowbird abundance (Stribley and Haufler 1999, Tewksbury et al. 1999, Young and Hutto 1999), and cowbird abundance and brood parasitism often increase with proximity to grazing (Robinson et al. 1995; Goguen and Mathews 1999, 2000; Morse and Robinson 1999). In areas where cowbirds are already abundant, breeding activities are often concentrated in the deciduous riparian zones where there is a high abundance and diversity of breeding birds (Szaro and Jakle 1985), especially when the riparian zone is adjacent to agricultural areas (Tewksbury et al. 1999).

Proximity to open habitats and streams is also reported to influence brood parasitism. Reports on how these factors influence brood parasitism vary among locations, host species, and habitats; patterns are not always predictable, and conflicting evidence can be found for many factors (Hahn and Hatfield 1995). There is some evidence that cowbirds are more abundant near the edge of a habitat (Brittingham and Temple 1983, Chalfoun et al. 2002), and specifically more abundant near the forest–stream edge (Gates and Giffen 1991). Other studies, however, have not found that parasitism is higher near the forest edge (Hahn and Hatfield 1995).

The structure and floristics of breeding habitat at the nest site and the position of the nest within the habitat may also affect the incidence of brood parasitism (Robinson et al. 1995). Nest concealment is associated with lower levels of parasitism in the Indigo Bunting (*Passerina cyanea*; Burhans 1997). Acadian Flycatcher (*E. virescens*) nests are more likely to be parasitized in habitats with a more open subcanopy and canopy (Brittingham and Temple 1996), and in lower nests (Wilson and Cooper 1998). In mixed oak–hickory forest in New York, low-nesting species are more likely to be parasitized than mid- to high-nesting species (Hahn and Hatfield 1995).

The main objective of this investigation was to identify factors that influence brood parasitism on *E. t. extimus*. Insights into which factors influence brood parasitism on the flycatcher are needed to inform decisions regarding policy and management for the flycatcher's recovery. We examined variation in the frequency of brood parasitism on nests of the endangered flycatcher in a valley that is predominantly grazed pasture. Given the reported relationship between grazing and parasitism risk and the importance of understanding the influences of grazing on this endangered subspecies, our first objective was to determine whether the distance of the nest to the nearest summer grazing influenced the likelihood of brood parasitism. Because the flycatcher's decline is attributed to loss and degradation of habitat and there is a great deal of interest in improving and restoring habitat specifically for the flycatcher, our second objective was to identify habitat characteristics that influence brood parasitism, including patch dimensions and microhabitat characteristics. Finally, because of conflicting reports of "edge effects" in other studies and a report of increased cowbird abundance on the forest–stream edge (Gates and Giffen 1991), our third objective was to evaluate the influence of nest location in relation to the patch edge—and, specifically, the riverside patch edge—on the frequency of brood parasitism.

Methods

Study site.—The study was conducted at two sites on the Gila River in southwest New Mexico: the Cliff-Gila Valley and the Gila River Bird Area. The population of flycatchers in the Cliff-Gila Valley is one of the largest known populations and the largest in New Mexico (Sedgwick 2000, USFWS 2002). The number of flycatchers breeding in the valley has fluctuated over the time of the present study (1997–2004) between an estimated high of 239 pairs to an estimated low of 125 pairs (K. M. Brodhead et al. unpubl. data). The Gila River Bird Area, which is ~15 km downstream from the Cliff-Gila Valley, supported 1–8 pairs each season.

The Cliff-Gila Valley has a well-developed floodplain in the low-gradient valley. Elevations range from 1,360 to 1,420 m. Much of the valley consists of irrigated and nonirrigated pastures used for grazing and hay farming. Cattle are excluded from most of the riparian patches during the breeding season, but many of the adjacent pastures are actively grazed. Riparian patches on the floodplain terraces are characterized by a mature Fremont cottonwood (*Populus fremontii*) overstory with a subcanopy dominated by stands of boxelder (*Acer negundo*) and Goodding's willow (*Salix gooddingii*). In many stands, boxelder is the most common tree, forming a closed subcanopy gallery forest. Young patches on low- to mid-elevation bars within the active river channel are Fremont cottonwood–Goodding's willow community type (Muldavin et al. 2000).

The Gila River Bird Area is located along ~5 km of the Gila River at the north end of the Big Burro Mountains. Elevations range from 1,315 to 1,345 m. The Bird Area is on public land administered by the Gila National Forest. Grazing at the site is limited to mainly the uplands during the dormant season (dates vary according to plant phenology), though floodplain pastures were grazed for two brief periods (time allotted depended on the site conditions) during that time. The river floodplain on the property adjacent to the forest boundary is accessible to cattle during the breeding season (820 m from the nearest recorded nest site). The riparian area is a Fremont cottonwood–Goodding's willow–Coyote willow (*Salix exigua*) community type (Muldavin et al. 2000).

Nest monitoring.—Data on nesting activities were collected from mid-May through August every year from 1997 through 2004. We conducted nest searches on a daily basis, and nests were monitored every three to seven days following, with modification, Rourke et al. (1999). Flycatcher behavior, nest activity, and nest contents were recorded on each visit. For nests below 5–6 m, nest contents were observed with pole-mounted mirrors or video cameras to ascertain nest stage and presence–absence of cowbird eggs or chicks. Because it is difficult to handle the poles above 5–6 m without potentially harming the nest and because tree climbing to check nests was too disruptive for an endangered species, high nests (~53% of total nests) were monitored with binoculars from a distance and the contents determined from adult activity at the nest. Repeated observations in the context of known nesting phenology (Sedgwick 2000) enabled us to ascertain nest stage and fate for most of the high nests. Brood parasitism in the high nests was established by visual or aural observation of cowbird nestlings or fledglings. We used all necessary precautions to minimize effects of disturbance when searching for and monitoring nests (Martin and Geupel 1993, Rourke et al. 1999). Brood parasitism was estimated as the number of nests that were confirmed as parasitized divided by the number of nests with known parasitism status.

Habitat sampling.—We sampled habitat characteristics at each nest site at the end of each season after the flycatchers had vacated their territories. For each nest, we recorded the height of the nest tree (THT), the height of the nest (NHT), the tree species used as substrate, the diameter of the nest-tree trunk at breast height (DBH), and Universal Transverse Mercator (UTM) coordinates. We used these measures to evaluate the correlation between nest-tree characteristics and the frequency of brood parasitism. All nests with a known parasitism status were used in the analyses.

Landscape calculations.—Using ARCGIS software (ARCMAP, version 8.2; ESRI, Redlands, California), we projected nest locations over U.S. Geological Survey digital orthoquads, delineated riparian patches and pastures that were grazed during the breeding season, and calculated variables of interest. The UTM nest locations were reviewed for accuracy. Riparian patches were defined as having a distinct boundary and no woody vegetation (e.g., pastures and gravel bars). The area and perimeter of each patch were estimated from the delineated features and added to the nest data as variables. Using the ARCGIS Spatial Analyst Extension, we calculated straight-line distances to grazing (GRZ) and to the patch edge (EDG) and captured the distance at each nest site as variables in the nest data.

Perimeter:area ratio (PAR), a simple index describing patch shape, was calculated from the perimeter and area values and added as a variable to the nest data. Patches with low PAR have more core area, whereas patches with greater PAR have greater perimeter lengths in relation to core area and a more convoluted shape. The PAR tends to decrease with patches of greater area, even when shape is held constant; therefore, it tests the influence of core quantity on the frequency of brood parasitism.

The flycatcher is associated with open water, and cowbirds can be more abundant near the forest–stream edge (Gates and Giffen 1991), so we determined whether a nest's location in relation to the river had any influence on brood parasitism. We quantified this by calculating the percentage of active river channel (the area between the river-channel banks) in a 50-m radius around the nest site. The percentage of active channel around a nest site was useful for defining its location in relation to the floodplain banks, which was comparable to the forest–stream edge. The areas with the highest percentages of active channel were within the channel banks and were characterized by young riparian patches and gravel bars, and the areas with the lowest percentages were farthest from the river banks and defined areas on the upland side of the mature riparian patches. We estimated the percentage of active river channel within 50 m using ARCGIS Spatial Analyst Extension.

Data analysis.—Logistic regression was used to evaluate the correlation between the binomially distributed parasitism data and each predictor (Neter et al. 1996, Agresti 2002). R, version 2.0.0, was used for all analyses (R Development Core Team 2003). Logistic regression coefficients were estimated using maximum likelihood. Odds ratios, which measure the probability of an event occurring at one measure of the predictor variable compared with the odds of its occurring after a one-unit increase in the predictor variable, and associated profile-likelihood 95% confidence intervals (CI; Agresti 2002), were employed to evaluate the strength and direction of each relationship. The significance of the parameter estimate was determined with the Z-statistic and was deemed as significant with $P < 0.05$. We also used contingency tables to compare the observed and expected number of nests parasitized in each tree species and tested for significant differences with Pearson's chi-square statistic (χ^2).

The plotted response functions (lowess) depicting the relationships between parasitism and patch area (PA) and parasitism and the percentage of active river channel (ARC) were not smooth, continuously increasing or decreasing shapes, an assumption of logistic regression (Neter et al. 1996). Rather than using the measurements as quantitative variables, we classified PA into categories of low, medium, or high, and ARC was classified into five categories of increasing value (Table 1). By treating the measurements as categorical variables, we were able to evaluate the proportion of parasitism within each category compared with the other categories, which was more appropriate than interpreting logistic regression parameters that would have been unable to define the irregular relationships. To select break points for the variable classes, we used the functionality of

Table 1. Summary of variables used as predictors of brood parasitism in logistic regression analyses.

	Code	n	Minimum	Maximum	Mean
Predictor					
Nest height (m)	NHT	480	1.0	24.1	6.4
Tree height (m)	THT	473	1.6	32.4	11.1
Trunk diameter at breast height (1.5 m) (cm)	DBH	472	0.5	142	26.8
Distance to grazing (m)	GRZ	491	0	811	219.3
Distance to patch edge (m)	EDG	491	1.0	68.0	19.6
Patch area (ha)	PA	491	0.01	7.84	4.85
Patch perimeter (10^2 m)	PP	491	0.4	40.9	24.4
Patch perimeter-area ratio	PAR	491	0.033	0.403	0.061
Active channel within 50 m (%)	ARC	491	0	100	32.0
Categorical predictor					
Active channel within 50 m (<12%)	ARC1	239	–	–	–
Active channel within 50 m (12–36%)	ARC2	63	–	–	–
Active channel within 50 m (37–60.5%)	ARC3	67	–	–	–
Active channel within 50 m (61–85%)	ARC4	50	–	–	–
Active channel within 50 m (>86%)	ARC5	72	–	–	–
Patch area—small (0–2.4 ha)	PA1	120	–	–	–
Patch area—medium (2.4–5.3 ha)	PA2	106	–	–	–
Patch Area—large (5.3–7.8 ha)	PA3	265	–	–	–

ARCMAP. Point data in ARCMAP can be classified according to natural clusters within the distribution of a data attribute (variable), which forms clusters by minimizing the squared deviations of class means.

We tested the influence of the categories of PA and ARC on parasitism by comparing the proportion of nests parasitized within each category and the associated 95% CI. When parasitism within one of the categories was higher or lower than in the population overall, we tested for significant differences in parasitism between this category and all the others combined, using an indicator variable (1 for the chosen category, 0 for all other categories) in logistic regression. The log-odds (logit) from logistic regression with an indicator variable as the predictor are reported in the results. The value of the log-odds for a single category is irrelevant (for indicator variables); the log-odds makes sense only by comparison with the value for another category (Agresti 2002). When the log-odds increases from one category to the next, it indicates that the odds of parasitism increase (and vice versa). We estimated odds-ratios from the log-odds, which, with indicator variables, are a ratio of the odds of brood parasitism between the two categories. When the log-odds is greater than one, the odds of parasitism in the first class are greater than the odds in the second class, and values less than one indicate that the odds of parasitism in the second class are greater.

We predicted that the relationship between selected continuous variables (NHT, THT, DBH, EDG, and PAR) and brood parasitism would vary depending on patch area. To test this, we ran logistic regression models with an interaction between the continuous and the indicator variable for patch area, which fit the probability of parasitism (response) to the continuous predictor separately for the two categories of patch area. Significant parameter estimates for the categorical variable denoted different effects on the fit between the two categories.

Forward stepwise variable selection was used for model building. The likelihood ratio statistic (LRT) was used to evaluate variable entry. Three models chosen by forward stepping were selected as competing models and subjected to further evaluation. Output from the stepwise procedure was assessed by interpretability, and alternative models were compared using Akaike's Information Criterion (AIC; Burnham and Anderson 1998). We only considered models that were based on sound ecological principles. Competing models all had a low number of parameters but remained effective in reducing deviance. Goodness-of-fit of the final logistic regression model was evaluated with (1) the Hosmer-Lemeshow statistic (Agresti 2002) and (2) influence diagnostics conducted using *Dfbeta* (Neter et al. 1996).

The parameters and variance structure of the final multivariate model were estimated under relaxed assumptions of independence using generalized estimating equations (GEE; Liang and Zeger 1986). Clumped distributions (Hatten and Paradzick 2003, Brodhead 2005) and small territories (Sedgwick and Knopf 1992, K. M. Brodhead et al. unpubl. data) are characteristic of breeding flycatcher distributions, and are factors that could influence assumptions of spatial independence among sample points. Use of GEE requires that clusters of potentially correlated data are identified, and we identified clusters as intersecting 70-m buffers around nest sites in ARCMAP. The resulting clusters included most of the nests within a patch but effectively excluded nests in other patches. The significance of the parameter estimates was assessed with the Wald statistic.

Flycatchers exhibit breeding-site fidelity (Sedgwick 2004), and the analysis of nest data over many years may be a potential violation of temporal independence. To assess model consistency between years and to address potential violations of temporal independence, the final regression model was re-evaluated after adding an interaction between an indicator variable coding for a given year and each variable in the model. This was repeated for every year of the study. Model consistency among years was checked for the final model.

Results

Brood parasitism.—The total proportion of nests parasitized across all years and for all locations was 20.2%, based on 491 flycatcher nests of known parasitism status (Table 2). Parasitism in each year varied from a low of 11.3% in 1997 to a high of 32.2% in 1998. We suggest that because higher nests were less susceptible to parasitism (see below), the frequency of parasitism may have been somewhat lower than we estimated

TABLE 2. Number of nests with known parasitism status (n), proportion of nests parasitized (BP), standard errors (SE), and confidence intervals (CI) by year.

Year	n	BP	SE	95% CI
1997	53	0.113	0.044	0.053 to 0.226
1998	59	0.322	0.061	0.217 to 0.449
1999	41	0.122	0.051	0.053 to 0.225
2000	44	0.136	0.052	0.064 to 0.267
2001	67	0.149	0.044	0.083 to 0.253
2002	79	0.253	0.049	0.170 to 0.359
2003	75	0.213	0.047	0.136 to 0.319
2004	72	0.236	0.05	0.153 to 0.346

because the mean height of the nests that were excluded from the analysis ($n = 420$) (parasitism status unknown) was 1.2 m higher than all of the nests combined. Of the parasitized nests, an estimated 19% were subsequently abandoned. However, it is likely that this percentage was, in fact, greater, because if we were unable to confirm the presence of a cowbird egg in a nest that was abandoned, the nest would have been marked as having unknown parasitism status and not included in the analysis. We recorded at least three parasitized nests that fledged both flycatcher and cowbird young from 2002 through 2004.

Habitat characteristics.—Brood parasitism varied by tree species used for nesting. Nests were built mainly in either boxelder or one of three species of willow (*S. gooddingii, S. irrorata, S. exigua*). Overall, nests built in boxelder were parasitized less than expected (Table 3). When evaluating the data by year, however, 2002 was the only year for which observed parasitism was significantly lower in boxelders ($P < 0.05$) and 2001 the only year for which observed parasitism was significantly greater in willows ($P = 0.03$, $n = 7$). Nests built in nonnative invasive tree species (*Tamarix* sp. and *Eleagnus angustifolia*) did not have a significantly different likelihood of being parasitized than nests in native vegetation.

Overall, parasitized nests were built lower in the tree (4.7 m ± 3.3 [SD]) than unparasitized nests (6.8 m ± 4.1) and in shorter trees (9.2 m ± 5.6) than unparasitized nests (11.7 m ± 5.5), and the trees with parasitized nests had smaller trunk diameters (13.4 cm ± 11.5) than trees with unparasitized nests (20.2 cm ± 17.4) (Table 4). As single predictor variables in logistic regression, NHT, THT, and DBH were negatively correlated

TABLE 3. Observed and expected counts of brood parasitism in nest-tree species by year. Significant differences between observed (obs) and expected (exp) rates are tested with Pearson's chi-square statistic (χ^2).

	Acer negundo					*Salix* spp.					Other				
	n	obs	exp	χ^2	P	n	obs	exp	χ^2	P	n	obs	exp	χ^2	P
1997	41	3	4.6	2.89	0.09	5	1	0.6	0.41	0.52	7	2	0.8	2.39	0.12
1998	41	13	13.0	0.47	0.79	10	4	3.2	0.34	0.56	8	2	2.6	0.22	0.64
1999	27	4	3.3	0.51	0.48	9	0	1.1	0.60	0.21	5	1	0.6	0.32	0.57
2000	35	4	4.8	0.71	0.40	2	1	0.3	2.34	0.13	7	1	1.0	<0.01	0.96
2001	50	5	7.5	3.77	0.05	7	3	1.1	4.80	0.03	10	2	1.5	0.24	0.63
2002	45	7	11.0	5.27	0.02	30	11	7.6	3.30	0.07	4	2	1.0	1.36	0.24
2003	37	7	7.9	0.25	0.62	30	6	6.4	0.05	0.82	8	3	1.7	0.05	0.82
2004	37	9	8.6	0.05	0.83	30	7	7.0	<0.01	0.99	6	1	1.4	0.16	0.69
Total	313	52	63.0	6.76	0.01	123	33	25.0	4.53	0.03	34	8	6.9	1.08	0.30

TABLE 4. Relative use and mean tree measurements for parasitized (1) and unparasitized (0) nests given for the various nesting substrate species. The F-statistic (analysis of deviance) tests the difference between mean values of tree variables between parasitized and unparasitized nests.

Tree species	*n*		Mean NHT (m)			Mean THT (m)			Mean DBH (cm)		
	1	0	1	0	F^a	1	0	F^a	1	0	F^a
Acer negundo	52	261	6.3	8.4	14.1***	12.2	14.1	7.7***	19.3	26.0	10.0**
Salix spp.	33	90	3.0	3.1	<0.1‡	6.0	5.8	0.1‡	6.1	6.0	0.0‡
Baccharis salicifolia	4	3	2.2	1.9	0.4‡	3.7	3.0	1.7‡	2.4	1.9	1.2‡
Populus fremontii	2	10	2.8	6.7	1.3‡	9.3	11.4	0.1‡	8.1	22.4	0.4‡
Alnus oblongifolia	2	5	2.6	5.9	3.6†	5.3	10.5	2.1‡	3.4	12.0	3.1†
Eleagnus angustifolia	4	10	4.0	4.9	0.4‡	5.8	8.2	2.8†	16.0	17.3	0.1‡
Tamarix ramosissima	2	7	2.5	2.9	0.4‡	3.4	8.3	3.4†	5.4	9.1	1.2‡
All species	99	386	4.7	6.8	23.5***	9.2	11.7	16.0***	13.4	20.2	17.0***

[a] Significance codes: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, † $P < 0.1$, and ‡ $P > 0.1$.

Abbreviations: NHT = nest height, THT = tree height, and DBH = diameter at breast height.

with the probability of brood parasitism (Table 5). However, we found that these relationships were primarily true only for boxelder but were not true for nests in willows (Table 4). Only 11.2% of nests were built in species other than boxelder and willows, which makes it difficult to detect significant differences with the small samples sizes; but in general, nests built in species other than willow and seepwillow (*Baccharis salicifolia*) followed the same pattern as boxelder, with lower nests parasitized in greater proportion.

Landscape characteristics.—The mean distance to grazing was lower for parasitized nests (194.7 ± 158.2) than for unparasitized nests (225.5 ± 185.7). However, although it defined a negative trend, the parameter estimate from single-variable logistic regression with GRZ as the predictor was not significantly different from zero ($P = 0.13$; Table 5).

Parasitized nests were built closer to the patch edge (17.6 m ± 12.2) than unparasitized nests (20.0 m ± 13.6), but although the sign of parameter estimate from logistic regression defined a negative trend between EDG and the probability of parasitism, the estimates were not significant (Table 5). There was a stronger relationship between EDG and brood parasitism, but it was dependent on the patch area (see below).

Brood parasitism did not appear to be significantly related to the PP or PAR. Mean PAR in parasitized nests (0.060 ± 0.043) was almost no different than mean PAR in unparasitized nests (0.061 ± 0.034), and mean PP in parasitized nests (25.0 ± 12.6) was only slightly higher than mean PP in unparasitized nests (24.3 ± 13.0). Logistic regression parameter estimates were not significantly different from zero ($P = 0.63$ and $P = 0.77$, respectively; Table 5).

The proportion of parasitized nests in high-area patches was greater (0.241; 95% CI: 0.193–0.295), and in medium-area patches lower (0.123; 95% CI: 0.073–0.199), than the proportion of parasitism in all nests combined (0.202; 95% CI: 0.169–0.239) (Fig. 1). Parasitism in small patches (0.185; 95% CI: 0.125–0.264) was not significantly different from the overall proportion of parasitized nests. A logistic regression model with category PA3 (see Table 1) coded as an indicator variable, where high area = 0 and low and medium area = 1, significantly improved the model fit ($P = 0.02$; Table 5). The odds ratio comparing the two categories of patch area indicates that the estimated odds of brood parasitism for

Table 5. Nest-site and patch variables used as single-variable predictors in logistic regression to model the frequency of brood parasitism. Parameter estimates (± SE) and *P*-values of the *Z*-statistic (*Z*) are given for each regression.

Predictor code[a]	Intercept	Estimate	*Z*	*P*(<|z|)	Odds ratio[b]	CI[c]
NHT	–0.470	–0.163 ± 0.037	–4.43	<0.001	0.85	0.79–0.91
THT	–0.454	–0.086 ± 0.022	–3.86	<0.001	0.92	0.88–0.96
DBH	–0.750	–0.036 ± 0.010	–3.70	<0.001	0.97	0.95–0.98
EDG	–1.109	–1.014 ± 0.009	–1.55	0.120	0.99	0.97–1.00
GRZ	–1.163	–0.001 ± 0.001	–1.51	0.131	1.00	1.00–1.00
PP	–1.480	0.004 ± 0.009	0.48	0.630	1.00	0.99–1.02
PAR	–1.318	0.000 ± 0.000	–0.30	0.767	1.00	0.99–1.00
PA3 (1)[d]	–1.144	– ± 0.233	–2.37	0.018	1.74	1.11–2.77
PA3 (0)[d]	–1.697	– ± 0.144	–7.97	<0.001		
ARC4 (1)[d]	–0.663	– ± 0.323	2.52	0.012	2.26	1.18–4.20
ARC4 (0)[d]	–1.477	– ± 0.122	–12.06	<0.001		
EDG*(PA3=1)	–0.577	–0.029 ± 0.012	–2.32	0.020	0.97	0.95–1.00
EDG*(PA3=0)	–1.678	–0.001 ± 0.019	1.52	0.129	0.98	0.94–1.06

[a] Predictor abbreviations are as given in Table 1.

[b] Odds ratio for continuous predictors is a ratio of the odds of occurrence at a given value of the variable and odds of occurrence at a one-unit increase of the variable. Odds ratios for indicator variables compare the odds of brood parasitism between the category on the row above and the category on the row below, and a value greater than one means that the category on the row above has a greater odds of being parasitized.

[c] Profile-likelihood-based 95% confidence intervals (Agresti 2002).

[d] The log-odds (logit) are reported in the intercept column for the logistic regressions run with indicator variables.

large area patches are 1.74× the estimated odds for low- and medium-area patches.

Nests built within a ~30-m strip of land just beyond the edge of the floodplain terrace (ARC4) were parasitized in greater proportion (0.340; 95% CI: 0.224–0.478), and nests that were farthest from the active river channel (ARC1, ARC2) were parasitized in lesser proportion (ARC1: 0.159; 95% CI: 0.089–0.268; ARC2: 0.172; 95% CI: 0.129–0.224) than all nests in the data pool (Fig. 1). Logistic regression parameter estimates for the indicator variables identifying these categories, however, were significant only for ARC4 (Table 5). The estimated odds of parasitism in category 4 were 2.25× greater than the estimated odds of parasitism for all the other classes combined (Table 5). ARC4 was a strong-performing predictor in the multivariate model; its addition improved the model fit significantly when evaluated by deviance reduction in model building. However, it was not retained in the final model, because its parameter estimate was not significant (*P* = 0.12).

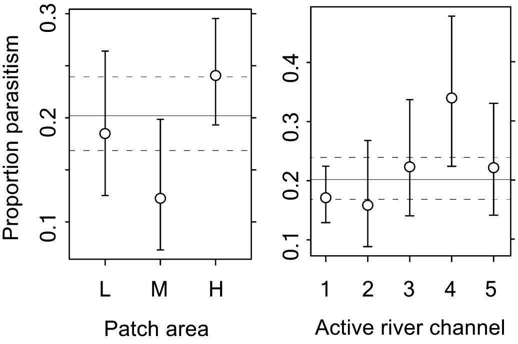

Fig. 1. Mean proportion of brood parasitism with 95% confidence intervals within each category of patch area and each category of active river channel. Overall estimated frequency of brood parasitism (0.202; horizontal line) and confidence intervals (dashed line) are displayed for comparison. Abbreviations for the predictors and values for each category are provided in Table 1.

The correlation between some of the continuous predictors and brood parasitism depended on patch area. The relationship between brood parasitism and distance to the edge of the patch was stronger where patch area was greater (Fig. 2). Parameter estimates obtained from a model with EDG as a continuous predictor and patch area coded as an indicator variable confirmed the significance of the relationship (Table 5). The

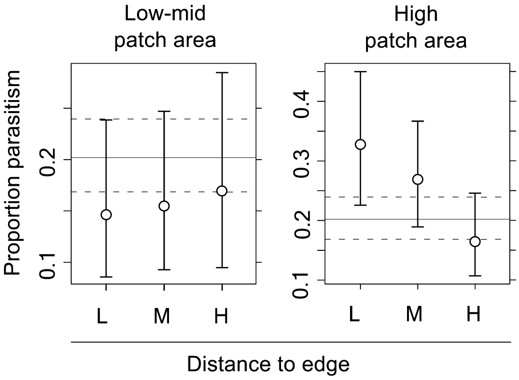

Fig. 2. Proportions of brood parasitism for nests near (<11.1 m), at a moderate distance from (11.2–22.3 m), and far from (>22.3 m) the patch edge, for patches with low to medium area (<5.3 ha) and high area (>5.3 ha), graphed with 95% confidence intervals. Overall estimated frequency of brood parasitism (0.202; horizontal line) and confidence intervals (dashed line) are displayed for comparison. Values for the patch-area categories are provided in Table 1.

sign and value of the parameter estimates indicated that for large patches, the probability of parasitism declined more rapidly as the distance to patch edge increased, but in small to medium patches, the rate of change in the probability of parasitism was close to zero: Log-odds$_{\text{high.area}}$ = –0.577 – 0.029 × EDG; Log-odds$_{\text{low-med.area}}$ = –1.678 – 0.001 × EDG.

Multivariate parasitism model.—The final model chosen by forward-stepping binomial regression retained the variables NHT, EDG, and PAR, and the indicator variable for the PA3 category as an interactive term. Parameter estimates, standard errors, and significance values are reported in Table 6. Parameter estimates came from generalized estimating equations, but they did not differ substantially from those obtained with logistic regression: Log-odds$_{\text{high.area}}$ = 2.30 – 0.143 × NHT – 0.033 × EDG – 42.0 × PAR; Log-odds$_{\text{low-med.area}}$ = –1.09 – 0.143 × NHT + 0.009 × EDG + 2.06 × PAR.

The difference between the parameter estimates for the two equations indicated that nests in patches of greater size were more likely to be parasitized. The odds ratio for the indicator variable was estimated with the mean values for NHT, EDG, and PAR and indicated that nests in larger patches have a 1.26× greater estimated odds of being parasitized than nests in smaller patches when all other variables are held at the average values.

Table 6. Parameter estimates (± SE) and *P*-values for the Wald statistic obtained from the generalized estimation equation fit of the data modeling the odds of brood parasitism.

Predictor[a]	Estimate	Wald	*P*
Intercept	–1.090 ± 0.589	3.43	0.064
NHT	–0.143 ± 0.042	11.80	0.001
EDG	0.009 ± 0.014	0.42	0.519
PA3	3.384 ± 1.194	8.03	0.005
PAR	2.063 ± 3.911	0.28	0.598
EDG*PA3	–0.042 ± 0.019	4.66	0.031
PAR*PA3	–44.086 ± 19.973	4.87	0.027

[a] Predictor abbreviations are as given in Table 1.

In patches >5.3 ha, the probability of brood parasitism declined as EDG increased. In large patches with low values of PAR (more core area), the probability of brood parasitism is greater. In patches <5.3 ha, however, neither EDG nor PAR have a convincing influence on brood parasitism.

We retained the final model after reviewing goodness-of-fit tests and model consistency between years, with the caveat that it performs well for predicting high frequencies of brood parasitism but is unable to predict very low frequencies of brood parasitism accurately. This indicates that there may be a threshold as to how protected from the threats of brood parasitism a given nest site can be at our study site.

Discussion

Our study defines conditions that make flycatcher breeding habitat more susceptible to brood parasitism in a southwestern riparian ecosystem. The results indicate that edge habitat, especially habitat on the riverside edge of a large patch with greater core area, is particularly prone to parasitism. High host densities seem to be characteristic of these conditions and may be an important underlying factor influencing the frequency of brood parasitism in riparian zones of the Southwest. Our results also suggest that brood parasitism is influenced more by characteristics of nesting habitat than by the distance to active grazing. With regard to these results, we suggest that cattle management focused on habitat condition (e.g., summer grazing exclusion from occupied flycatcher habitat) may be more beneficial than cattle management targeted at influencing cowbird abundance (e.g., grazing restrictions based on a set distance to occupied flycatcher habitat). We discuss these points in detail in the following discussion.

In the present study, levels of brood parasitism are greater near habitat edge in larger patches. The edge effect we show is in agreement with studies of parasitism in a wide variety of habitat types (Brittingham and Temple 1983, Tewksbury et al. 1998, Morse and Robinson 1999, Chalfoun et al. 2002). Contrary to our results, some studies have shown that nests farther from the edge are more susceptible to parasitism (Hahn and Hatfield 1995, Burhans and Thompson 1999). Burhans and Thompson (1999), however, defined a patch as "interlocking leafy vegetation," whereas we define a patch as continuous riparian habitat bounded on all sides by an open field or gravel bar; therefore, the results from the two studies are not comparable. Although Hahn and Hatfield (1995) showed that brood parasitism increases in the forest interior, they emphasized that parasitism–edge patterns are complex, varying with location, and cannot be interpreted simply.

Inconsistent support for edge effects with brood parasitism might be a result of variation in habitat type, but it may be that some underlying factor is responsible for the perceived edge effect, such as greater host density. Although lower forest cover can be a significant predictor of brood parasitism, the density of host species is a stronger predictor in the same system (Tewksbury et al. 1998). Gates and Giffen (1991) reported a higher density of cowbirds near stream edge, where there is a high density of breeding birds. Similarly, the present study shows an increased frequency of parasitism near the edge of the floodplain terrace on the river side of the patches. These locales are likely to have greater structural variation, because they are near water and protected from flooding and, therefore, can support both new growth and older trees. Structural variation is a habitat characteristic that is associated with greater faunal species diversity, especially for riparian birds (e.g., Rice et al. 1983). It follows that there may be greater host diversity and that the parasitism edge effect that we observed is, in part, driven by greater host density within the edge habitat adjacent to the river.

In our study, patch area is positively correlated with brood parasitism. Similarly, Burhans and Thompson (1999) showed that nests of Yellow-breasted Chat (*Icteria virens*) in larger patches are more likely to be parasitized. We suggest a few reasonable explanations for this relationship. It may be that larger patches are more attractive to cowbirds because of a greater potential number of hosts, given that cowbird abundance is positively correlated with host densities (Robinson et al. 1995, Tewksbury et al. 1998, Tewksbury et al. 1999) and bird species richness (Chace 2004). Larger patches may contain a greater abundance and variety of potential nest sites, thereby attracting greater numbers and diversity of birds. A greater number of host species favored by the cowbird may be more abundant in larger patches than in small patches. Hahn and Hatfield (1995) used similar reasoning in suggesting that the lack of a parasitism-edge effect in their study might be a result of a preference for hosts that breed in the forest interior. Lastly, larger patches may have habitat characteristics that cowbirds prefer. Burhans and Thompson (1999) offered a similar suggestion, hypothesizing that brood-parasitism levels would be higher for nests closer to greater numbers of trees because the trees offer nest-searching perches for the cowbird.

Although our study shows patch area to be positively correlated with brood parasitism, larger patches support multilayered, heterogeneous canopies, which may provide for more successful nesting and survival overall. Higher host densities could be an indication of high-quality habitat. There are a greater number of potential nest sites in patches with higher foliage density, and greater canopy cover in the area surrounding a nest may offer better concealment and thus a lower probability of predation (Martin and Roper 1988). In Burhans and Thompson's study (1999) on Yellow-breasted Chats, the loss to parasitism in larger patches was offset by greater nesting success, because the mean number of young fledged was equivalent in large and small patches. Indeed, eight studies that were reviewed by Paton (1994) all demonstrate, with one minor exception, that nest success is greater in larger patches.

Presence of livestock.—Cowbirds associate with cattle, and some evidence shows that, in some systems, increasing the distance from a nest to active grazing reduces the probability of parasitism (Goguen and Mathews 2000, Kostecke et al. 2003). Our results do not provide strong support for this relationship and are in agreement with two studies from the middle Rio Grande in New Mexico. The Rio Grande studies show that the presence or absence of cattle does not significantly influence female cowbird densities (Tisdale-Hein and Knight 2003) and that cowbird movements do not differ between grazed and ungrazed sites, because cowbirds remain in areas with high concentrations of hosts (Sechrist and Ahlers 2003). Broad floodplains in the Southwest are more likely to support breeding flycatchers (Hatten and Paradzick 2003), provide abundant human-based food sources for cowbirds, and support high densities of breeding birds (Szaro and Jakle 1985). Therefore, exclusion of livestock from floodplains may have little or no effect in reducing parasitism. The results that show a reduction in brood parasitism with greater distance to cattle come from studies of upland sites rather than floodplains, which may account for the apparent discrepancy.

The weak influence of the distance to grazing on the frequency of brood parasitism shown here might have been stronger had our scale of analysis been greater. The maximum distance to grazing of any given nest at our study site was <1 km. If our data set had included a greater range of predictor values, the positive relationship between grazing and parasitism might have been significant. There is evidence, however, that the minimum distance from grazing to a nest required for a significant decline in brood parasitism may be too great to be a practical option for management. After a reduction in cattle stocking rates, female cowbirds commute greater distances between foraging and breeding sites (Kostecke et al. 2003). In upland habitats, cowbirds commute up to 7 km (Rothstein et al. 1984) or 8 km (Goguen and Mathews 2000) between breeding and foraging areas.

It is important also to consider how much parasitism affects seasonal fecundity and a species' population growth rate. Measures of brood parasitism based on individual nests do not take into account the outcome of renesting attempts by the same pair and can, therefore, overestimate the negative effects of parasitism on seasonal fecundity and the population growth rate (Pease and Grzybowski 1995, Schmidt and Whelan 1999). As an example, although brood parasitism declined after removing cattle in Goguen and Mathews's study (2000), nest success was unaffected. There is still much to be learned about the relationship between population viability and brood parasitism, but most recent literature on the flycatcher urges caution before controlling cowbirds to benefit flycatcher populations and suggests that any actions should first be evaluated on a site-specific basis (Sedgwick 2000, USFWS 2002, Rothstein et al. 2003). In many cases, cowbird parasitism may not be a primary threat to larger populations as long as adequate habitat is available and productivity is high enough to offset the adverse affects (Sedgwick and Iko 1999, Rothstein et al. 2003).

Conservation implications.—We contend that, in most cases, cattle management should focus on reducing effects on the health of riparian habitat rather than on removing cattle to reduce the threat of brood parasitism by cowbirds. Our results show that habitat characteristics influence the frequency of brood parasitism, and recent literature discussing effects of brood parasitism on the flycatcher advise that habitat health is a greater concern for its recovery than cowbird management (Sedgwick 2000, Rothstein et al. 2003). In addition, there is a great deal of mistrust of regulatory actions of the government in regard to conservation within social landscapes of the rural West (e.g., Brook et al. 2003), and mandating the removal of cattle far enough from affected riparian corridors to preclude parasitism would likely generate resentment (see Davis 2001). Such mandates could also accelerate the development of ranchlands into rural subdivisions, which is a problem with its own ecological costs (Knight et al. 1995; see Jensen 2001). There is critical need for partnerships and cooperation between ranchers and government agencies, and encouraging stewardship of the land, including cattle management aimed at improving riparian areas, is apt to be a more effective approach for long-term conservation.

We suggest that habitat management is of paramount importance for recovering a healthy population of the flycatcher. Through restoration efforts in our study site, revegetation of healthy riparian habitat now supports breeding flycatchers (see Boucher et al. 2003). Grazing in the riparian zone during the growing season can have a negative effect on riparian condition (Kauffman and Krueger 1984, Sedgwick and Knopf 1991, Jansen and Robertson 2001), and cattle removal can lead to the recovery of riparian vegetation and bird populations (Kreuper et al. 2003). Livestock management strategies that seek to reduce the negative effects of grazing on riparian health should be examined, such as grazing only during the nongrowing season (Kauffman and Krueger 1984, Knopf et al. 1988, Sedgwick and Knopf 1991). Cattle are generally excluded from most of the flycatcher breeding sites within our study site during the breeding season; however, much of it is winter grazed. Given the potential detrimental effects of grazing during the growing season on riparian health, and our results showing that the frequency of parasitism is influenced by characteristics of the habitat, we recommend that increasing the amount of flycatcher habitats and improving the condition of nesting habitat and the suitability of nest substrates should be emphasized in efforts to recover the flycatcher.

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