Riparian habitat disturbed by reservoir management does not function as an ecological trap for the Yellow Warbler (*Setophaga petechia*)

S.P. Quinlan and D.J. Green

Abstract: Ecological traps arise when anthropogenic change creates habitat that appears suitable but when selected reduces the fitness of an individual. We evaluated whether riparian habitat within the drawdown zone of the Arrow Lakes Reservoir, British Columbia, creates an ecological trap for Yellow Warblers (*Setophaga petechia* (L., 1766)) by investigating habitat preferences and the fitness consequences of habitat selection decisions. Preferences were inferred by examining how habitat variables influenced settlement order, and comparing habitat at nest sites and random locations. Males preferred to settle in territories with more riparian shrub and tree cover, higher shrub diversity, and less high canopy cover. Females built nests in taller shrubs surrounded by a greater density of shrub stems. Habitat preferences were positively associated with fitness: nest sites in taller shrubs surrounded by higher shrub-stem densities were more likely to avoid predation and fledge young, whereas territories with more riparian cover, higher shrub diversity, and less high canopy cover had higher annual productivity. We therefore found no evidence that riparian habitat affected by reservoir operations functions as an ecological trap. Current habitat selection decisions may be associated with fitness because Yellow Warblers are adapted to breeding in a heterogeneous environment subject to periodic flooding.

Key words: riparian, Yellow Warbler, *Setophaga petechia*, habitat selection, ecological trap, reservoir.

Résumé : Les pièges écologiques existent lorsque des changements anthropiques créent un habitat qui semble adéquat mais qui réduit la fitness de l'individu qui le choisit. Nous évaluons si l'habitat riverain dans la zone de marnage du réservoir d'Arrow Lakes, Colombie-Britannique, forme un piège écologique pour les parulines jaunes (*Setophaga petechia* (L., 1766)) en étudiant les préférences d'habitat et les conséquences pour la fitness des décisions de choix d'habitat. Nous déduisons les préférences en examinant comment les variables de l'habitat influencent l'ordre des établissements et en comparant l'habitat des sites de nidification à celui de sites choisis au hasard. Les mâles préfèrent s'établir dans des territoires qui ont une couverture riveraine plus importante de buissons et d'arbres, une diversité plus élevée de buissons et une densité moins grande du haut couvert forestier. Les femelles construisent leur nid dans les buissons plus élevés, entourés par une densité plus importante de tiges de buissons. Il y a une association positive entre les préférences d'habitat et la fitness; les sites de nidification dans les buissons plus élevés entourés d'une densité plus grande de tiges de buissons sont plus susceptibles d'éliminer la prédation et de permettre l'envol des petits; les sites avec une couverture riveraine plus dense, une diversité plus grande des buissons et un haut couvert forestier moins dense ont une productivité annuelle plus forte. Nous ne trouvons donc aucune indication que l'habitat riverain affecté par le fonctionnement du réservoir agit comme piège écologue. Les décisions actuelles de choix d'habitat peuvent être associées à la fitness parce que les parulines jaunes sont adaptées à se reproduire dans un milieu hétérogène sujet à des inondations périodiques.

Mots-clés : habitat riverain, paruline jaune, *Setophaga petechia*, sélection d'habitat, piège écologique, réservoir.

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Introduction

Models of habitat selection tend to assume that individuals have evolved to recognize and settle preferentially in the highest quality habitat available (Fretwell and Lucas 1969; Fretwell 1972). Settlement decisions are therefore thought to be influenced by environmental cues that reliably predict reproductive success and survival (Clark and Shutler 1999; Stamps and Krishnan 2005). For example, individuals may select habitat based on food availability (Morris and MacEachern 2010), the risk of predation (Parejo and Avilés 2011) or the density of brood parasites (Forsman and Martin 2009). However, in many cases the factors that determine productivity or survival may not be evident at the time habitat is selected, forcing individuals to use indirect cues to evaluate habitat quality. In recently modified environments, indirect cues can become uncoupled from the true quality of the habitat so that preferred habitats are less productive than other habitats available, creating an ecological trap (Dwernychuk and Boag 1972; Gates and Gysel 1978; Robertson and

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Hutto 2006). Nonideal habitat selection decisions in modified environments may also arise if individuals show no preference among habitats that differ in quality ("equal-preference traps"; Robertson and Hutto 2006) or actively avoid high-quality habitat ("perceptual traps"; Patten and Kelly 2010).

Ecological traps are thought to be more common in modified environments where human activities introduce new competitors or predators, change agricultural practices, or change other types of land use (Gates and Gysel 1978; Schlaepfer et al. 2002; Battin 2004). Ecological traps may therefore contribute to population declines of species occupying disturbed habitat (Battin 2004), and theoretically can lead to local extirpation if initial population sizes are low (Pulliam and Danielson 1991; Delibes et al. 2001; Donovan and Thompson 2001; Kristan 2003). However, strong empirical evidence for the existence of ecological traps remains limited. This may be because ecological traps are rare and restricted to heavily modified environments (Robertson and Hutto 2006). Alternatively, the lack of evidence for ecological traps has been attributed to difficulties in measuring habitat preferences of individuals (Robertson and Hutto 2006), the need to link apparent cues to reliable fitness estimates (Arlt and Part 2007), or because the links between habitat preferences and fitness outcomes are measured at the wrong spatial scales (Kristan 2003).

The majority of empirical studies investigating the concept of ecological traps in birds have used relative density or use-availability data to infer habitat preferences and nest success to estimate fitness (Robertson and Hutto 2006). However, using relative density to determine habitat preferences has been criticized, as many factors can influence the number of individuals within a particular habitat (Robertson and Hutto 2006; Part et al. 2007). Tracking individual decision-making is a more direct and potentially more reliable method of gathering information about habitat preference. For example, several studies on migratory birds have used the order in which territories are occupied in the spring to examine habitat preferences (e.g., Arlt and Part 2007; Harrison and Green 2010). Nest success and the number of fledglings produced during a nesting attempt provides information on predation rates and food availability within a habitat (Martin 1993) and is directly linked to individual fitness. However, in some species, pairs may re-nest after failure or double brood, and consequently, annual productivity provides a more precise estimate of the fitness consequences of particular habitat selection decisions.

We investigated habitat preferences and the fitness consequences of habitat selection decisions made by Yellow Warblers (*Setophaga petechia* (L., 1766)) breeding in riparian habitat affected by reservoir operations on the Columbia River, British Columbia, Canada. Many riparian-dependent songbirds, including Yellow Warblers, have declined in abundance on breeding bird survey routes across North America (Environment Canada 2010). Habitat loss and degradation has been implicated in these population declines (DeSante and George 1994; Sanders and Edge 1998). Locally, dams on the Columbia River have led to the loss of more than 87% of the riparian habitat within the Canadian portion of the Columbia River (Moody et al. 2007). However, nonideal habitat selection decisions in the remaining modified riparian habitat could exacerbate the impact of habitat loss and degradation on populations of Yellow Warblers.

We evaluated habitat preferences of Yellow Warblers by examining habitat selection decisions operating during settlement and during nest-site selection. We examined the fitness consequences of these decisions, and the mechanism linking habitat preference and individual fitness, by examining how habitat features that influenced settlement order and nest-site selection influenced brood parasitism, nest predation, nest success, and annual productivity. We tested the following hypotheses: (*i*) habitat variables influence the order in which territories are settled, (*ii*) habitat surrounding nest sites differs from habitat surrounding random points, and (*iii*) habitat variables that influence settlement order and the location of nest sites are linked to fitness. We predicted that (*i*) if riparian habitat along the Columbia River, modified by alteration to water flow and affected by water-use decisions in the Arrow Lake Reservoir system, functions as an ecological trap, then habitat variables associated with preference would be negatively related to nest success and annual productivity; (*ii*) if riparian habitat functions as an equal-preference or perceptual trap, then habitat variables associated with improved nest success or higher productivity would not influence habitat selection or would be associated with habitat avoidance, respectively.

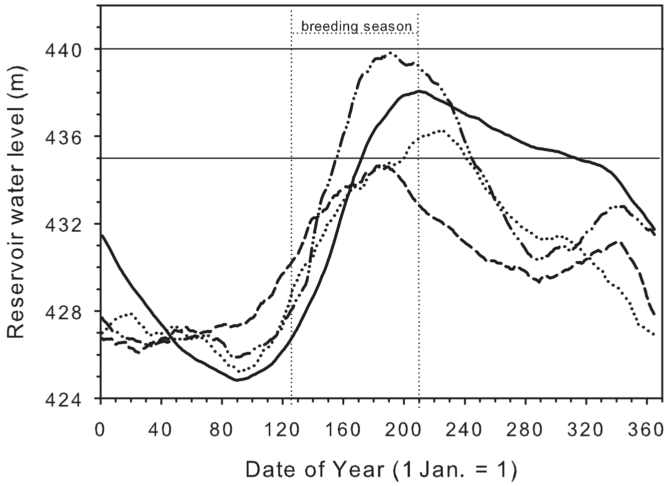
Materials and methods

Species and study area

Yellow Warblers are one of the most common passerine species breeding in wet, deciduous habitats within the Northern Rockies (Tewksbury et al. 2002) and the species is recognized as a management indicator of subcanopy and shrub habitats in riparian areas by the USDA Forest Service and Partners in Flight. Breeding bird surveys suggest that populations of Yellow Warblers in British Columbia and the Northern Rockies have declined by 1.9% per year over the last four decades (Environment Canada 2010). Loss and degradation of habitat leading to higher nest predation and parasitism are cited as the main causes of declines among western populations (DeSante and George 1994; Sauer et al. 1996; Ortega and Ortega 2000). However, Saracco et al. (2008) argued that adult survival may also be an important driver of recent population trends in some regions.

We monitored habitat selection and breeding of Yellow Warblers in Revelstoke Reach (50.97°N, 118.20°W), which is situated within the drawdown zone of Arrow Lakes Reservoir, a 240 km long reservoir system in the upper Columbia River Valley. Water levels in the reservoir, formed in 1968 after the downstream construction of the 52 m high Hugh Keenleyside Dam, range in elevation (above sea level) from 422 to 440 m. We established three study plots, 30–39 ha in size, in riparian habitat located in the upper reaches of the floodplain (435–441 m) that are periodically disturbed by inundation owing to downstream reservoir operations (Fig. 1). Riparian habitat at the three study plots included stands of mature black cottonwood (*Populus balsamifera* L.) with a diverse understorey of dogwood (*Cornus sericea* ssp. *sericea* L.), snowberry (*Symphoricarpos albus* (L.) S.F. Blake), black twinberry (*Lonicera involucrata* (Richardson) Banks ex Spreng.), and willow (genus *Salix* L.), narrow strips of 20-

Fig. 1. Seasonal variation in water levels in the Arrow Lakes Reservoir, British Columbia, Canada. Solid line shows the mean daily water level for 1968–2010. Water levels are also shown for 2004 (dotted line), 2005 (dashed line), and 2006 (dot–dash line). Horizontal lines indicate maximum allowable pool for the reservoir (440 m) and lowest elevation for deciduous tree or shrub habitat within the drawdown zone of the reservoir (435 m).



to 30-year-old cottonwood forest adjacent to upland coniferous forest, willow-dominated scrub, and isolated patches of willow within a matrix of open grass habitat.

Monitoring arrival dates and breeding performance

All three plots were monitored throughout the breeding season beginning in late April, when migrant birds are observed moving north through the Columbia River valley, until late July in 2004 to 2006. Each site was surveyed systematically every 1–2 days to determine when males returned to establish breeding territories, band new arrivals, and map breeding territories. Returning males are easily identifiable because they sing from prominent perches immediately upon arrival and aggressively defend territories by chasing other conspecifics (Studd and Robertson 1988). We attempted to catch all territorial males within 1–2 days of their return to the study area. Territories were mapped by following males and recording the locations of singing posts and points of boundary disputes with neighbours. Females were typically caught later as they moved to and from the nest. All birds were banded with a numbered metal Canadian Wildlife Service issued band and a unique combination of three colour bands. The majority of territorial males were banded at all three sites (80% in 2004 and 100% in 2005 and 2006). We recorded the arrival date of all males and the order in which territories were occupied.

We observed pairs and monitored all breeding attempts from mid-May to late July. Nests were typically located by following females while nest-building. Nests were checked daily during egg-laying to determine when clutches were initiated (defined here as the first egg laid by the female), document occurrences of brood-parasitism and record clutch size. Nests were subsequently checked every 2–4 days to determine hatch dates, brood sizes, fledging success or the cause of nest failure. Nests that could not be checked with the aid of a stepladder and pole-mounted mirror were monitored from a distance with a spotting scope. Where possible, nestlings were weighed and banded on day 7 of the 9-day nestling period. We assumed nests fledged all young banded or observed at nests on day 7 if there were no signs of predation and parents were subsequently observed defending or feeding fledglings within their territory. Nests were considered successful if they fledged at least one young. The annual productivity of a pair was defined as the sum of fledged young from all nesting attempts within a season.

Habitat characteristics of territories and nest locations

We determined the habitat characteristics of each territory by measuring the structure, cover, and composition of vegetation surrounding each nest built by a breeding pair. We examined nest site selection by comparing the vegetation surrounding nest sites and random locations within each study plot. Random locations were chosen by generating random UTM coordinates within each study plot and centred on the nearest suitable nesting substrate (shrub or tree) to this coordinate. Random location were forced to be more than 20m from previously selected random points to reduce repeated sampling of the same habitat and maximize coverage of available habitat (Boyce 2006).

Habitat characteristics surrounding all nests and random points were measured at the end of each breeding season. Vegetation was measured using a modified BBIRD vegetation sampling design for shrub/ground nesting passerines (Martin et al. 1997). We measured a total of 12 habitat variables (Table 1). We quantified the shrub layer within 5 m radius plots, and forest composition and structure within 11.3 m radius plots centred on the nest or random points. We also quantified the overall riparian (shrub or tree) habitat cover and number of riparian tree or shrub habitat patches within a 50 m radius of the nest or random point using a digitized vegetation map of the study area and the GIS software package ArcView version 5.1 (Environmental Systems Research Institute (ESRI), Inc., Redlands, California, USA). We chose a 50 m radius as this results in an area that approximates the size of the larger yellow warbler territories in this study (0.47 ± 0.19 ha (mean ± SD), range 0.21–0.96, $n = 38$ territories in 2006).

Statistical analyses

Preliminary examination of our data resulted in the elimination of two habitat variables from subsequent analyses; the number of coniferous trees was uninformative, as there were typically zero conifers surrounding nests or random points, and the number of deciduous trees was a redundant variable, as it was positively correlated ($r_S > 0.7$) with mean canopy height and high canopy cover.

We first used a linear mixed model to examine how habitat influenced the order in which territories were settled. Male identity was initially entered as a random term. However, there was little variance associated with male identity (estimated variance components were close to zero with considerably larger standard errors), so we simplified our analysis by dropping the random term. Our full model included eight habitat variables (Table 1). We used mean values to define the habitat characteristics of a territory if pairs initiated more than one breeding attempt during a year. Our final minimal model was obtained by sequentially removing nonsignificant

Table 1. Habitat variables measured at nest sites of Yellow Warblers (*Setophaga petechia*) and random locations within Revelstoke Reach in 2004–2006.

Habitat variable	Unit	Description
Nest substrate height[a]	m	Height of actual or potential nesting substrate
Distance to edge[a]	m	Distance from plot centre to grassland matrix
Understory cover	%	Canopy cover <5 m measured using a densiometer
High canopy cover	%	Canopy cover >5 m measured using a densiometer
Shrub stem density	No.	Number of deciduous stems <8 cm diameter at breast height (dbh) within a 5 m radius of the plot centre
Shrub diversity	No.	Number of genera of shrubs within a 5 m radius of the plot centre
Forb cover	%	Visual estimation of % cover of forbs within a 5 m radius of the plot centre
No. of deciduous trees[b]	No.	Number of deciduous tress >8 cm dbh within a 11.3 m radius of the plot centre
No. of coniferous trees[b]	No.	Number of coniferous trees >8 cm dbh within a 11.3 m radius of the plot centre
Mean canopy height	m	Mean height of the canopy within a 11.3 m radius of the plot centre
Riparian habitat cover[c]	%	Percent riparian shrub or tree cover within 50 m radius of the plot centre estimated using a digitized vegetation map of the study area
No. of riparian habitat patches[c]	No.	Number of distinct patches of riparian shrub or tree habitat >7 m^2 within a 50 m radius of the plot centre

[a] Excluded from models examining settlement order.

[b] Redundant or uninformative variable excluded from all analyses.

[c] Excluded from discriminant function analysis.

terms until only significant terms remained. Significance was assessed using the change in deviance (which approximates to a χ^2 distribution) associated with dropping the term from a more complete model. Variables that had been dropped were back-checked against the minimal model to ensure that order effects did not influence the final model selected.

We used a multivariate discriminant function analysis (DFA) to evaluate which habitat variables were most useful in discriminating between nest sites of Yellow Warblers (n = 76) and random locations (n = 65) within the riparian habitat in our study plots. We only included data from first nesting attempts to avoid over-representation of selected habitat. We included eight variables in this analysis (Table 1), excluding the two variables that quantified habitat at the territory rather than nest scale (percent riparian habitat and patchiness). A forward stepwise DFA was used to select the most useful subset of discriminating variables. At each step, the variable that minimized the overall Wilks' λ and added to the overall discrimination (F-to-enter, $P < 0.05$) was added to the model and selected variables were removed if they no longer contributed to the discrimination (F-to-remove, $P < 0.1$). We tested the significance of the final DFA using the model Wilks' λ and determined the relative importance of the selected habitat variables by examining the magnitude of the standardized canonical correlation coefficients (McGarigal et al. 2000).

We used generalized linear mixed models, with either a binomial distribution and logit link or a Poisson distribution and log link, to examine how habitat variables influenced brood parasitism (0 or 1), predation (0 or 1), nest failure (0 or 1), and seasonal productivity. The latter analysis used mean habitat values if females built more than one nest in any given year. Female identity was initially entered as a random term in all models but was subsequently dropped, as there was little variance associated with the random term. Full models included all 10 variables in analyses related to nest success and 8 variables in analyses of productivity (Table 1). The latter analysis excluded the two variables only relevant to nest sites (substrate height and distance to the grassland edge). Final models were selected by sequentially removing nonsignificant terms until only significant terms remained. Significance was assessed using either the Wald statistic or the change in deviance associated with dropping the term from a more complete model. Variables that had been dropped were back-checked against the minimal model to ensure that order effects did not influence the final model selected. Habitat variables associated with settlement could influence seasonal productivity simply because birds that arrive early are older and (or) of higher quality. Our final analysis therefore examined whether controlling for settlement order alters conclusions about how habitat influences seasonal productivity. In all models, we examine diagnostic plots to confirm assumptions about normality and variance. Statistical analyses were performed in Genstat version 13.0 (VSN International, Hemel Hempstead, UK) and SPSS version 16 (SPSS Inc., Chicago, Illinois, USA).

Results

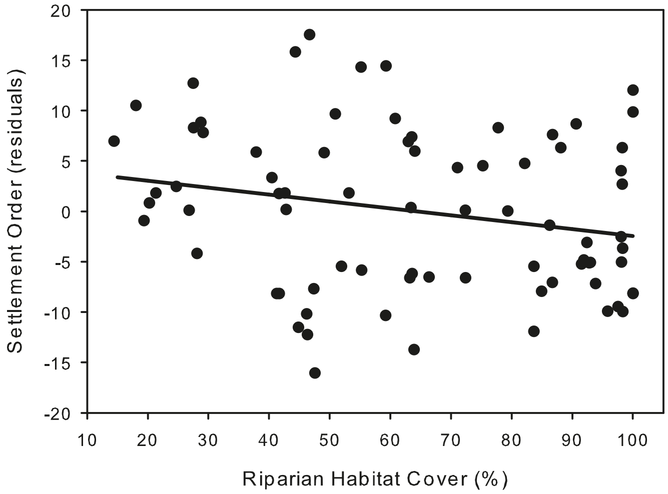
Settlement decisions of male Yellow Warblers

Males returned to the study area over a 3–4 week period between 5 May and the first week in June. Having settled on a territory, males maintained these territories throughout the breeding season. Three habitat variables influenced the order in which territories were occupied. Males settled earlier in territories with a higher percentage of riparian habitat cover (Fig. 2; $\chi^2_{[1]} = 5.32$, $P = 0.02$). Males also settled earlier in territories with a greater diversity of shrubs ($\chi^2_{[1]} = 4.22$, $P = 0.04$) and less high canopy cover ($\chi^2_{[1]} = 12.8$, $P < 0.001$). The order in which territories were settled was not related to any other habitat variable (all $P > 0.30$).

Nest-site selection by Yellow Warblers

There was considerable variation in the habitat surrounding nesting locations within territories of Yellow Warblers and random points within our three study sites (Table 2). Two

Fig. 2. Relationship between riparian habitat cover (percent riparian shrub or tree habitat cover within a 50 m radius) and settlement order residuals (controlling for the effects of shrub diversity and high canopy cover) by Yellow Warblers (*Setophaga petechia*) breeding in Revelstoke, British Columbia, Canada.



habitat variables, shrub stem density and substrate height, helped discriminate between points centred on nests and random points (model Wilks' λ = 0.77, $\chi^2_{[2]} = 34.8$, $P < 0.001$). Shrub stem density made the greater contribution to the discriminant function having a standardized canonical coefficient of 1.02 and a canonical loading of 0.91. Substrate height had a standardized canonical coefficient of 0.43 and a canonical loading of 0.17. Nests were in taller shrubs or trees than potential nesting substrates and were surrounded by a higher density of shrub stems than random sites. The discriminant function classified 71% of the nest sites and 75% of the random sites correctly.

Nesting success

We monitored the fate and collected habitat data for 96 nesting attempts made by 78 different pairs (2004, $n = 22$; 2005, $n = 36$; 2006, $n = 38$). Brown-headed Cowbirds (*Molothrus ater* (Boddaert, 1783)) parasitized 29% of the nests checked ($n = 86$; two nests were excluded after being abandoned during laying for unknown reasons and eight nests could not be accessed). None of the habitat variables that influenced the order in which territories were settled or that were implicated in nest-site selection influenced whether nests were parasitized (percent riparian habitat cover, $\chi^2_{[1]} = 0.00$, $P = 0.95$; shrub diversity, $\chi^2_{[1]} = 0.11$, $P = 0.75$; canopy cover, $\chi^2_{[1]} = 0.93$, $P = 0.34$; shrub stem density, $\chi^2_{[1]} = 0.34$, $P = 0.58$; substrate height, $\chi^2_{[1]} = 1.50$, $P = 0.22$). Brood parasitism was also unrelated to any of the other habitat variables measured (all $P > 0.25$).

Predation resulted in the loss of 33% of nests where clutches were initiated and nests were not abandoned as a result of parasitism by Brown-headed Cowbirds or unknown events ($n = 87$). Both habitat variables implicated in nest-site selection also influenced nest predation. Nests were less likely to be depredated if they were built in taller substrates ($\chi^2_{[1]} = 10.2$, $P = 0.001$) and surrounded by a higher density of shrub stems ($\chi^2_{[1]} = 9.1$, $P = 0.003$). None of the variables that influenced the order in which territories were settled influenced nest predation (percent riparian habitat cover, $\chi^2_{[1]} = 2.9$, $P = 0.09$; shrub diversity, $\chi^2_{[1]} = 2.22$, $P = 0.14$; canopy cover, $\chi^2_{[1]} = 0.28$, $P = 0.60$). Nests were also less likely to be depredated in territories with a greater number of riparian shrub or tree habitat patches ($\chi^2_{[1]} = 13.2$, $P < 0.001$). No other habitat variables influenced nest predation (all $P > 0.25$).

Overall, 59% of nests monitored as part of this study ($n = 96$) fledged at least one Yellow Warbler. Nest failure was attributed to predation ($n = 25$), nest abandonment following parasitism by Brown-headed Cowbirds ($n = 7$) or other disturbance ($n = 2$), flooding owing to reservoir operations ($n = 3$), the use of yellow warbler nest material by cedar waxwings (*Bombycilla cedrorum* Vieillot, 1808) ($n = 1$), and unknown causes ($n = 1$). Nest success was positively influenced by substrate height ($\chi^2_{[1]} = 4.19$, $P = 0.04$) and shrub stem density (Fig. 3; $\chi^2_{[1]} = 4.17$, $P = 0.04$). No other habitat variables had a significant effect on nest success (all $P > 0.05$).

Annual productivity

We collected habitat data and monitored the annual productivity of Yellow Warblers breeding on 77 territories (2004, $n = 19$; 2005, $n = 24$; 2006, $n = 34$). The majority of these territories were occupied by pairs; one territory was occupied by a male and two females. Territories occupied by pairs produced 2.41 ± 1.99 (mean ± SD) young and the territory occupied by the polygynous male fledged 6 young over the course of the season. Annual productivity of territories occupied by pairs was related to all three variables that influenced settlement order; percent riparian habitat cover and shrub diversity were positively related to productivity (percent riparian habitat cover, $\chi^2_{[1]} = 8.84$, $P = 0.003$; shrub diversity, $\chi^2_{[1]} = 5.88$, $P = 0.02$), and high canopy cover had a negative relationship with productivity ($\chi^2_{[1]} = 4.53$, $P = 0.03$). Annual productivity was also higher in territories with more patches of riparian shrub or tree habitat ($\chi^2_{[1]} = 4.91$, $P = 0.03$). No other habitat variables influenced annual productivity (all $P > 0.30$). Productivity could be related to the habitat variables associated with settlement order simply because birds that occupy territories that are settled first are older and (or) of higher quality. After controlling for settlement order, annual productivity still increased with the amount of riparian habitat cover and the number of riparian patches (Fig. 4; percent riparian habitat cover, $\chi^2_{[1]} = 11.7$, $P = 0.001$; no. of patches, $\chi^2_{[1]} = 7.60$, $P = 0.006$) but was not influenced by shrub diversity ($\chi^2_{[1]} = 2.34$, $P = 0.13$) or high canopy cover ($\chi^2_{[1]} = 0.35$, $P = 0.55$).

Discussion

Indirect cues used in habitat selection can become decoupled from habitat quality in recently modified environments and create a situation where animals prefer to settle in a habitat with a lower fitness pay-off than could be obtained if they used an alternative habitat (Battin 2004). However, we found no evidence that settlement decisions of Yellow Warblers would cause riparian habitat affected by reservoir operations to function as an ecological, equal-preference, or

Table 2. Mean values and 95% confidence intervals (CI) for habitat variables sampled at points centred on nests (n = 76) of Yellow warblers (*Setophaga petechia*) and random points (n = 65) within the study plots in Revelstoke Reach, British Columbia, Canada.

	Nests			Random points		
		95% CI			95% CI	
Habitat variable	Mean	Lower	Upper	Mean	Lower	Upper
Nest substrate height (m)	5.7	4.3	7.1	4.7	3.6	5.8
Distance to edge (m)	21.8	16.4	27.2	11.1	6.9	15.3
Understory cover (%)	46.3	34.6	58.0	36.8	25.6	48.0
High canopy cover (%)	19.6	14.4	24.8	25.5	17.8	33.2
Shrub stem density	249	214	284	120	95	145
Shrub diversity	3.2	2.6	3.8	2.9	2.3	3.5
Forb cover (%)	3.8	2.9	4.7	2.6	1.8	3.4
No. of deciduous trees[a]	5.2	3.0	7.4	7.8	4.8	10.8
No. of coniferous trees[a]	0.4	0	0.8	0.3	0	0.6
Mean canopy height	7.1	5.8	8.4	8.1	6.4	9.8

[a] Redundant or uninformative variable excluded from all analyses.

Fig. 3. Relationship between shrub stem density surrounding a nest site (no. of stems within a 5 m radius) and nest success (likelihood that a nest where a clutch is initiated fledges at least one young). Line shows the predicted relationship from the final model, ln(P/1 – P) = –1.195 + 0.163(substrate height) + 0.003(shrub stem density), where substrate height is fixed at 3.5 m the median value in the data set. The points show the likelihood for the raw data binned into bins of 100 stems and the numbers show the sample size in each bin.

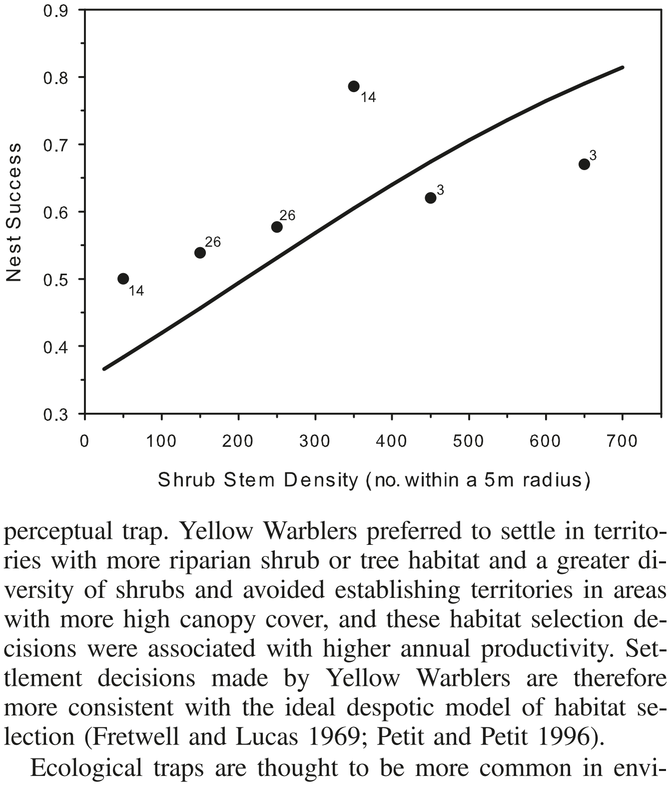
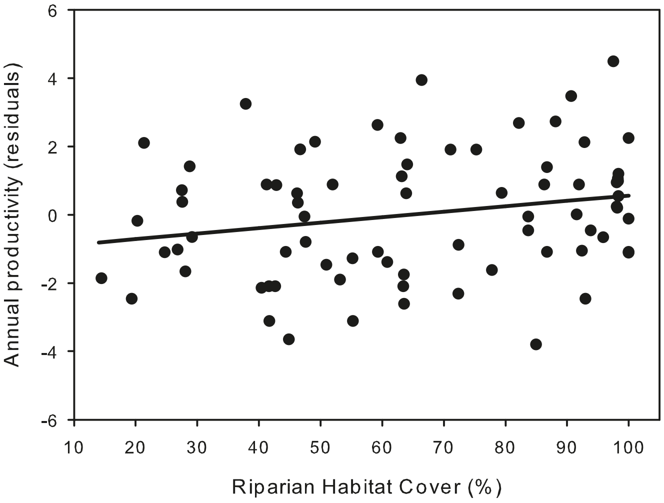


Fig. 4. Relationship between riparian habitat cover (percent riparian shrub or tree habitat within a 50 m radius) and annual productivity residuals (controlling for the order territories are settled and the number of riparian habitat patches) of Yellow Warblers (*Setophaga petechia*) breeding in Revelstoke, British Columbia, Canada.



perceptual trap. Yellow Warblers preferred to settle in territories with more riparian shrub or tree habitat and a greater diversity of shrubs and avoided establishing territories in areas with more high canopy cover, and these habitat selection decisions were associated with higher annual productivity. Settlement decisions made by Yellow Warblers are therefore more consistent with the ideal despotic model of habitat selection (Fretwell and Lucas 1969; Petit and Petit 1996).

Ecological traps are thought to be more common in environments modified by human activities (Schlaepfer et al. 2002; Battin 2004). Riparian ecosystems are among the most affected by humans; dams that regulate water for agricultural, industrial, and domestic purposes, hydroelectric power generation, and flood control have caused global-scale changes in riparian ecosystems (Poff et al. 1997; Nilsson and Berggren 2000). Upstream habitat can be lost or degraded as a result of inundation. The extent to which inundation affects habitat depends on the timing, degree, and length of inundation (van Eck et al. 2006; Vreugdenhil et al. 2006; Ström et al. 2011), but inundation can lead to reduced nesting success and declines in some bird populations (Reitan and Thingstad 1999). For example, inundation resulted in vegetation die-off within the Roosevelt Lake Reservoir, Arizona, that reduced tree densities, lowered canopy cover, and created more canopy gaps. Inundation consequently reduced nesting success and the number of Southwestern Willow Flycatchers (*Empidonax traillii extimus* A.R. Phillips, 1948) breeding in riparian habitat (Ellis et al. 2009). We expected that riparian habitat within reservoir systems would function as an ecological trap because apparently suitable riparian habitat can be flooded as a result of reservoir operations and reservoir operations could alter the distribution, abundance, and impact of nest predators and brood parasites. Counter to expectations, however, we found no evidence that habitat selection decisions by Yellow Warblers could create a situation in which riparian habitat within the drawdown zone of the Arrow Lakes would function as an ecological trap.

Equal-preference traps, where no habitat preferences are exhibited despite differences in habitat quality (e.g., Robertson and Hutto 2006; Powell et al. 2010), or perceptual traps, where animals actively avoid high-quality habitat (e.g., Patten and Bolger 2003), also have implications for population demography and carrying capacity (Gilroy and Sutherland 2007; Patten and Kelly 2010). In our study, Yellow Warbler exhibited no preference for territories with more patches of riparian shrub or tree habitat even though patch number had a positive effect on annual productivity. Males could potentially enhance their fitness by selecting sites with both more patches and higher overall riparian cover. Males may not incorporate patch number in settlement decisions because using total riparian cover, which is correlated with patch number, provides information on both habitat features. Alternatively, males may not select habitat based on the number of habitat patches because patch number has negative impacts on juvenile or adult survival that counterbalance the positive impacts on productivity.

Our study raises the question of how cues used to assess habitat quality and linked to fitness outcomes for Yellow Warbler in the past continue to be adaptive in a heavily modified environment. Two explanations appear plausible. First, riparian ecosystems are naturally dynamic and subject to periodic flooding that scours habitat, removing older trees and snags, transporting sediment and seeds, and promoting regeneration of riparian species such as cottonwoods and willow (Poff et al. 1997). Yellow Warblers may therefore be adapted to breeding in habitat subject to disturbance so that cues appropriate in riparian habitat with natural flow regimes remain appropriate when flow regimes have been modified. Second, habitat selection decisions may continue to be linked to annual productivity for Yellow Warblers in this reservoir system, because reservoir water levels do not typically rise until late in the breeding season and nests rarely failed owing to flooding. Habitat selection decisions of other species more vulnerable to inundation because they nest on the ground or breed later in the year may be more likely to be uncoupled from fitness outcomes.

Avian habitat selection is generally thought to be a hierarchical process with different cues and processes operating at different spatial scales (Hilden 1965; Orians and Wittenberger 1991). For example, Black-backed Woodpeckers (*Picoides arcticus* (Swainson, 1832)) select territories using cues that reflect food availability within a 250 m radius, select nesting habitat based on the density of pine and aspen snags within a 12.5 m radius, and select nest trees based on the species and condition of the tree (Bonnot et al. 2009). Habitat selection by Yellow Warblers also appeared to be hierarchical with the selection of territories being related to the amount of riparian shrub or tree cover measured at a territory scale and the selection of nest sites being influenced by shrub density and substrate height measured at the 5 m and nest-site scale, respectively. The cues that Yellow Warblers used to select territories were adaptive, possibly because they reflect food availability for this shrub-dependant foliage-gleaning insectivore, as annual productivity was higher on territories with greater riparian cover. The link between habitat preferences at a territory scale and fitness measured as productivity over the entire breeding season emphasize the importance of evaluating the concept of ecological traps using measures of preference and fitness outcomes collected at the appropriate spatial and temporal scale (Kristan 2003; Chalfoun and Martin 2007). Although outside the scope of this study, future work may also benefit from evaluating the role of landscape-level habitat characteristics as relationships between habitat preference and fitness outcomes can be dependent on factors operating at a larger scale (e.g., Cornell and Donovan 2010).

Yellow Warblers are thought to select nest sites based primarily on the characteristics of vegetation within a patch rather than on characteristics of the nesting substrate (Knopf and Sedgwick 1992). Knopf and Sedgwick (1992) argued that Yellow Warblers in Colorado preferred to nest in areas that contain a high density of uniformly sized willow bushes because these traits would favour nest concealment from nest predators and brood parasites. Consistent with their work, we found that Yellow Warblers built nests in taller than average bushes and preferred nest sites surrounded by a high density of shrub stems. Selection of nest sites based on these traits will be favoured by natural selection at our study site, as these traits influence nest predation, the primary source of nest failure in Yellow Warblers breeding in Revelstoke Reach. Nest cameras placed near fake or inactive nest of Yellow Warblers baited with eggs of Zebra Finch (*Taeniopygia guttata* (Vieillot, 1817)) identified American Crows (*Corvus brachyrhynchos* Brehm, 1822) as the principal nest predator at our study site (Rock 2011). Natural selection may favour different nest-site selection decisions in regions where brood parasitism rates are high and vary with nest location or where the predator community is dominated by mammalian rather than avian predators (Rangen et al. 1999, Sharp and Kus 2006).

In summary, although riparian habitat on the Columbia River has been heavily modified by hydroelectric development, our study suggests that the remaining riparian habitat within the drawdown zone of the Arrow Lakes Reservoir does not function as an ecological trap for Yellow Warblers. Habitat selection decisions operating during territory settlement and nest-site selection improve nesting success and annual productivity of Yellow Warblers that breed in riparian habitat influenced by reservoir water levels. However, further studies are required before concluding that reservoir operations do not create riparian habitat that acts as an ecological trap for other bird species. Savannah Sparrows (*Passerculus sandwichensis* (Gmelin, 1789)), which nest on the ground in grassland habitat at lower elevations within the drawdown zone, and Willow Flycatchers, which breed in willow shrub habitat from mid-June through August (H. van Oort, personal communication), are two local species where habitat preferences may currently lead to lower productivity and survival.

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