



Dynamics of habitat selection in birds: adaptive response to nest predation depends on multiple factors

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Abstract

According to theory, habitat selection by organisms should reflect underlying habitat-specific fitness consequences and, in birds, reproductive success has a strong impact on population growth in many species. Understanding processes affecting habitat selection also is critically important for guiding conservation initiatives. Northern pintails (*Anas acuta*) are migratory, temperate-nesting birds that breed in greatest concentrations in the prairies of North America and their population remains below conservation goals. Habitat loss and changing land use practices may have decoupled formerly reliable fitness cues with respect to nest habitat choices. We used data from 62 waterfowl nesting study sites across prairie Canada (1997–2009) to examine nest survival, a primary fitness metric, at multiple scales, in combination with estimates of habitat selection (i.e., nests versus random points), to test for evidence of adaptive habitat choices. We used the same habitat covariates in both analyses. Pintail nest survival varied with nest initiation date, nest habitat, pintail breeding pair density, landscape composition and annual moisture. Selection of nesting habitat reflected patterns in nest survival in some cases, indicating adaptive selection, but strength of habitat selection varied seasonally and depended on population density and landscape composition. Adaptive selection was most evident late in the breeding season, at low breeding densities and in cropland-dominated landscapes. Strikingly, at high breeding density, habitat choice appears to become maladaptive relative to nest predation. At larger spatial scales, the relative availability of habitats with low versus high nest survival, and changing land use practices, may limit the reproductive potential of pintails.

Keywords Agroecosystems · Habitat use · Conservation · Reproductive success · Northern pintail

Introduction

Theory suggests that animals should evolve behaviors to respond to variation in the availability of resources in space and time (e.g., migration, food-caching, nomadism, and habitat selection) such that patterns of resource use reflect underlying variation in fitness (Rosenzweig 1974; Orians and Wittenberger 1991). Thus, in the absence of disrupting cues, high use may be anticipated across scales where expected survival and/or reproductive success are high. Because a priori knowledge of actual fitness among sites is typically unavailable, individuals presumably have evolved the ability to identify proximate cues that reliably reflect fitness at scales that are important (e.g., Martin 1998; hereafter adaptive habitat selection). Across species and taxa, however, evidence for adaptive habitat selection is mixed (Clark and Shutler 1999; Misenhelter and Rotenberry 2000; Arlt and Pärt 2007; Chalfoun and Martin 2007). Non-correspondence with theory may occur where habitat choice

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is maladaptive as in ecological or evolutionary traps (e.g., Dwernychuk and Boag 1972, Schlaepfer et al. 2002) or perceptual traps (Patten and Kelly 2010). While understanding fitness cues and realized fitness is important in developing and testing behavioral ecology theory, it also has applied utility for conservation since environment-mediated demographic processes often regulate natural populations (Puliam 1996).

Clark and Shutler (1999) encouraged researchers to first identify the fitness consequences of habitat choice as a precursor to predictions regarding adaptive habitat selection. For birds, selection of nest sites, especially for ground-nesting species, can have important ramifications for reproductive success given the vulnerable nature of nests and potential risks to attendant parents (Martin 1993; Newton 1998; Arnold et al. 2012). Further, anthropogenic land use can affect vegetative structure, associated biota, and disturbance regimes at multiple scales (Opdam and Wiens 2002) with direct and indirect effects on reproductive success or survival at site, patch, or surrounding landscape scales (e.g., Battin and Lawler 2006). Nest survival is a frequently used surrogate for reproductive success in birds because this vital rate has important ramifications for population growth (Ricklefs 1969; Nagy and Holmes 2004). Thus, examination of habitat selection relative to variation in nest survival should provide insight into adaptive habitat selection in birds.

Northern pintails (*A. acuta*; hereafter, pintail) are migratory dabbling ducks well suited to evaluating predictions arising from habitat selection theory. Pintails breed in the greatest concentrations on the North American prairies, a landscape that has undergone dramatic alteration due to agricultural production. Pintails are unique among North American dabbling ducks in their nomadic wanderings in response to varying wetland conditions, and use of diverse nesting habitats, ranging from bare soil to thick vegetation (Clark et al. 2014) with known differences in expected nest survival (e.g., Klett et al. 1988). Persistently low populations since the 1980's have sparked concerns regarding the potential for detrimental interactions between land use, habitat selection, reproductive success, and survival (Miller and Duncan 1999; Podrutzny et al. 2002). While evidence for reproductive advantages of nest habitat selection in ducks is mixed (e.g., Clark and Shutler 1999; Richkus 2002), anthropogenic land use impacts on pintail nest survival, in conjunction with nest site selection, have been suggested as creating an ecological trap for this species (Miller and Duncan 1999).

Thus, our central objective is to test predictions arising from alternative hypotheses about how multi-scale patterns of pintail habitat selection are related to nest survival—we generally predict habitat selection will reflect patterns in nest survival. At the nest level, we examine pintail nest survival relative to distance to habitat edges with the prediction that pintails will distribute their nests further from habitat edges

than expected by chance (Livezey 1981; Stephens et al. 2005). Given seasonal variation in nest survival (Emery et al. 2005), we predict selection among habitats may vary with nest initiation date. At the patch scale, we predict habitats with greater nest concealment, and larger patches, will be preferred given evidence of higher nest survival in these situations (Higgins 1977; Klett et al. 1988; Greenwood et al. 1995; Sovada et al. 2000; Stephens et al. 2005).

While we do not examine pintail selection among landscapes, we predicted landscape-scale variables affecting nest survival could affect selection among nest habitats within landscapes. We predicted habitat selection could vary with breeding population density of both pintails and other waterfowl given potential density-dependent mechanisms affecting nest survival (Weller 1979; Minot 1981; Ims 1990; Larivière and Messier 1998). We predicted monotonic declines in nest survival if disturbance or competition was the mechanism, but lowest nest survival at moderate densities if predator swamping mediates predation at high breeding densities (Ims 1990). We predicted habitat selection may be less adaptive at high population density as explained below. We expected nest survival would be lower in cropland-dominated landscapes (Reynolds et al. 2001, Stephens et al. 2005) most likely due to differences in predator communities and foraging efficiency (Sargeant et al. 1993; Greenwood et al. 1995; Sovada et al. 2000) with knock on effects for habitat selection. Similarly, given predators in prairie landscapes forage extensively around wetlands (Larivière and Messier 2000; Phillips et al. 2003), we predicted nest survival would be lower in high wetland density landscapes with potential interacting effects on habitat selection. These predictions are reasonable given a functional response in habitat selection can depend on availability of habitats (e.g., Myrsterud and Ims 1998). Finally, because nest survival tends to be higher in wet versus dry years (Greenwood et al. 1995; Walker et al. 2013), we predicted annual moisture may interact with habitat selection in potentially adaptive ways.

Materials and methods

Study area

We used data obtained during three multi-year nesting studies conducted in prairie Canada by Ducks Unlimited Canada (DUC; Prairie Habitat Joint Venture [PHJV] Assessment Study, 1993–2000; Pintail Study, 2005–2007; Spatial/Temporal Variability Study [SPATS] 2001–2011), collectively designed to inform and improve delivery of habitat conservation programs. PHJV Assessment Study areas were single sites, 64 km² in size, where duck nesting ecology was studied at each site for 1 year only (Howerter et al. 2014). Pintail Study and SPATS designs included

clusters (hereafter, site-clusters) of 6–41 km² study areas stratified by percent grassland composition; two replicates each of low (<30%), moderate (30–60%), and high (>60%) grassland area. Each site cluster was examined for 1 or 2 years. From all studies, we included only sites, or site-clusters, where ≥ 20 pintail nests were found per year. In total, ten site-clusters and three PHJV sites, representing 62 study areas (1997–2009), were included.

Most study areas were located in the grassland ecoregions (Fescue, Mixed, and Moist Mixed Grasslands) of Alberta and Saskatchewan but three study areas were located in the Aspen Parkland ecoregion (Fig. 1). Landform in this region is characterized by flat to hummocky or kettle topography formed by lacustrine deposits and deposition of glacial till (Ecological Stratification Working Group 1995). Because these studies were focused on finding duck nests, study area locations generally were randomly selected within regions of moderate to high wetland densities in the form of ponds and shallow lakes (Stewart and Kantrud 1971; DUC unpublished data). Among study areas, wetland habitat averaged 12.7% (range 4–39%) of the area within study area boundaries. Primary land uses included cropland (predominantly for cereal grain and oil seed production), and introduced and native grass forage lands (pasture and haylands) for cattle production.

Breeding pair surveys

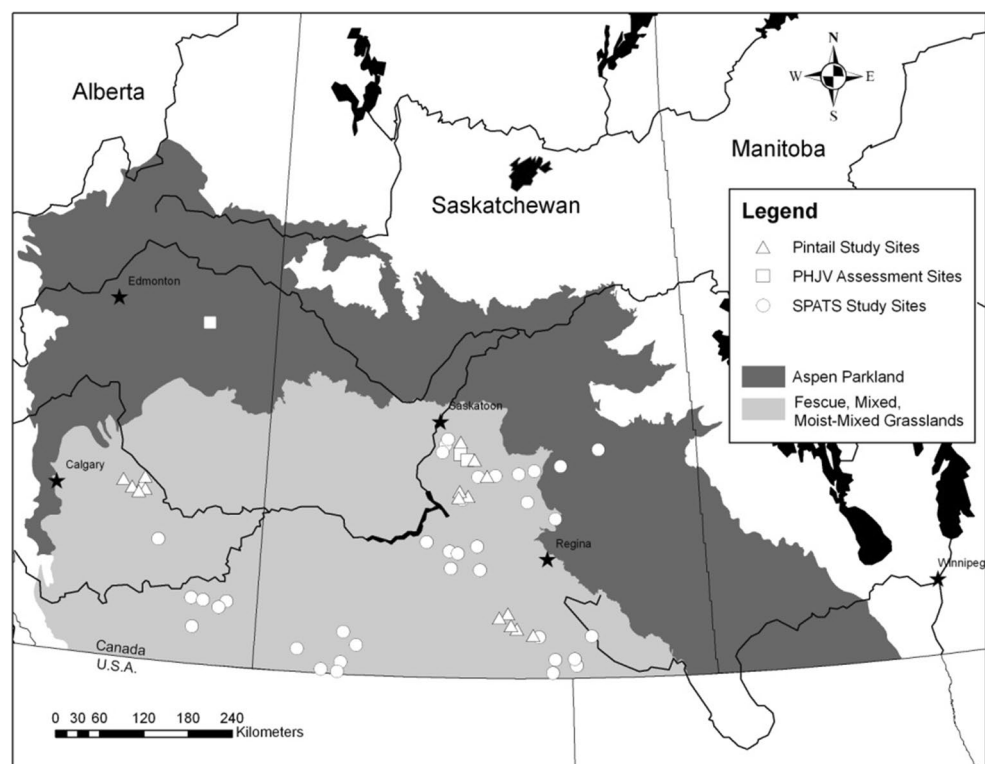
Ground-based duck counts (Dzubin 1969) were conducted at least twice on all study areas to estimate breeding pair densities for both early- and late-arriving species. Early surveys occurred during late April–early May (for mallard and pintail), and late surveys occurred in late May (for other duck species). Generally, surveys were completed between 0800 and 1400 h and were postponed during periods of high winds, fog, heavy rain or other low visibility conditions.

On PHJV Assessment and SPATS sites, wetlands were surveyed on foot (among-study area range: 1.8–2.7 and 0.2–2.6 km² surveyed wetland area, respectively). On Pintail Study areas, bi-weekly roadside surveys (Sauder et al. 1971) counted waterfowl on wetlands within 200 m of all roads within 1.6 km of study area boundaries (0.5–1.7 km² surveyed wetland area). Estimation of indicated breeding pairs followed Dzubin (1969) and pair densities are expressed as indicated breeding pairs km⁻² of wetland area surveyed. While both roadside and walking pair counts were conducted among studies, both methods are expected to provide similar results (Pagano and Arnold 2010).

Locating and monitoring waterfowl nests

Among studies, three or four nest searches were conducted at 3-week intervals from late April through mid-July following the procedures of Klett et al. (1986). Nests were found

Fig. 1 Location of Pintail, Prairie Habitat Joint Venture (PHJV) Assessment, and Spatial and Temporal Nesting Study (SPATS) sites within the Grassland and Aspen Parkland Ecozones of southern Alberta and Saskatchewan, 1997–2009



by dragging a 30 m cable-chain assembly, or a 2.5 cm × 75 m rope, between two all-terrain vehicles (ATV) through habitats being searched (Higgins et al. 1977). The ATV rope-drag was typically used in growing crops to minimize damage. Where ATV use was not practical, a 1 cm × 30 m rope was dragged between observers on foot, or lone observers walked and struck vegetation with willow switches to flush female ducks from nests. A nest was defined as a nest bowl with ≥ 1 egg attended by a female when found (Klett et al. 1986). Nest searches were conducted 6 days per week between 0700 and 1300 h when most laying and incubating females are expected to be tending nests (Gloutney et al. 1993). Searches were suspended during heavy rain. All habitat types were searched except trees, and flooded wetland vegetation. All areas searched were recorded on aerial photographs and later digitized in ArcMap (ArcGIS; ESRI, Redlands, CA).

When a nest was discovered, the habitat patch type, duck species, and number of eggs were recorded and incubation status was determined by field candling (Weller 1956). Nest location was recorded using GPS for later analyses in ArcMap and nests were marked with a flagged willow stake placed 4 m north of the nest to facilitate relocation. Nests were revisited at 7–10-day intervals until nest fate (successful, failed, or abandoned) was determined. If the scheduled revisit was within 2 days of estimated hatch, we revisited the nest 2–3 days after the estimated hatch date to avoid separating the female from recently hatched ducklings. A successful nest was defined as hatching ≥ 1 egg as indicated by the presence of shell membranes (Klett et al. 1986) or ducklings in the nest bowl. Failed nests were

indicated by evidence of abandonment or predation. When nests were abandoned on the first revisit following discovery (i.e., hen absent and no change in number of eggs or incubation), abandonment was attributed to investigator activity.

We excluded from nest survival calculations nests that were abandoned due to investigator disturbance at the time of discovery, fully or partially destroyed by investigators, or could not be relocated, but we included these nests in estimation of nest habitat preference ($n = 2$). Clutch initiation date was estimated by subtracting the age of the nest when found (i.e., number of eggs plus days of incubation) from the date of discovery (Klett et al. 1986).

Habitat classification and digitizing

We used a 6-class habitat definition scheme to describe a combination of vegetative and land-use characteristics typically used in many waterfowl nesting studies (e.g., Klett et al. 1988; Table 1). Habitat types were digitized in ArcMap from several imagery sources including 1:5,000 or 1:10,000 color or black and white infrared aerial photos and 2.5 m panchromatic SPOT images (SPOT Image Corporation, Chantilly, VA). All imagery was taken in May–August of the year of investigation (aerial photos) or May or June of the previous year (SPOT). All habitats within study area boundaries were ground-truthed in June and July of the year of investigation. We used ArcMap to extract from the digitized habitat layers various nest, patch, and landscape habitat covariates for use in analyses.

Table 1 Description of habitat types (HAB) used in the analysis of pintail nest survival and habitat preference at study areas in Alberta and Saskatchewan, 1997–2009. Labels used in presentation of results are provided in parentheses

Habitat type	Description
Spring cropland (SPRCROP)	Areas that are planted to small grains (e.g., wheat, barley), oilseeds (e.g., canola), or row crops (e.g., corn, soybeans) in the spring, or that retain previous year's crop stubble and are fallowed (tillage or chemical) during the growing season. Nesting cover remains uniformly sparse through much of the nesting season (mid-April–late June)
Fall cropland (FALCROP)	Croplands that are seeded and germinate in the fall, go dormant over the winter, and grow to maturity the following spring and summer (e.g., winter wheat and fall rye). Provides uniformly sparse nesting cover early in the nesting season but becomes tall and dense by early June
Grassland—idle (GRASSIDLE)	Areas vegetated with various mixtures of native and/or introduced grasses, forbs, and shrubs (aerial cover of trees and shrubs $\leq 30\%$) and have not been disturbed by haying, mowing, or grazing. Generally provides dense nesting cover throughout the nesting season
Grassland—grazed (PASTURE)	Areas vegetated with various mixtures of native and/or introduced grasses, forbs, and shrubs (aerial cover of trees and shrubs $\leq 30\%$) that have been primarily disturbed by grazing (may contain some hayed or mowed lands but exclude lands specifically planted for hay—see Hayland). Referred to as 'pasture grasslands' in text. Nesting cover in pasture is generally a heterogeneous mix of sparse and medium height cover
Hayland (HAYLAND)	Areas that have been seeded to grass and/or legume mixtures for forage production and that are hayed annually. Haylands provided uniformly sparse cover early in the nesting season but dense cover by early June
Wetland (WETLAND)	All areas, regardless of size, mapped as wetland according to definitions in Cowardin et al. (1979). Wetlands may be idled, grazed or hayed. Nesting cover is provided in generally dense, dry wetland vegetation around the basin margins

Nest survival analysis

We used a general likelihood specification in PROC NLMIXED (SAS Institute) to examine the influence of covariates on nest survival probability and used a logistic link function to model daily survival rate (DSR) as a transformably linear function of covariates (Dinsmore et al. 2002). We included the random effect of study site or site-cluster to account for unmodelled differences in DSR among years and geographic locations.

First, we assembled covariates that potentially explained variation in pintail nest survival, selected on the basis of previous research and plausible hypotheses (described above). Then, we constructed sets of *a priori* models containing covariates of potential importance at nest, habitat patch, and landscape scales. Where covariates measured related phenomenon (e.g., distance to wetland, and distance to habitat edge), or where covariates were correlated ($r > 0.5$), we included them separately in competing models. Full models included additive covariate main effects and selected within- and between-scale interactions that seemed plausible or tested specific hypotheses.

Nest-level covariates included nest age in days, clutch initiation date (IDATE; days since January 1), and distances (m) to nearest wetland (DISTWET) and habitat edges (DISTEDGE; Livezey 1981; Dinsmore et al. 2002; Emery et al. 2005; Stephens et al. 2005). At the patch scale, we considered categorical habitat type (HAB), and patch size in hectares (PATCHSZ). We use common agricultural landscape habitat type definitions that incorporate vegetation and land use information related to nest concealment potential, and anthropogenic disturbance, respectively (Table 1; e.g., Higgins 1977; Greenwood et al. 1995; Devries et al. 2008).

We considered five landscape-level variables (i.e., 41 or 64 km²) that we predicted affect nest survival as described above. We included the density of breeding pintail pairs alone (PINDEN), and breeding duck pairs excluding pintails (DUCKDEN). We included the percent of the landscape in cropland (PCTCROP) as a measure of the intensity of agricultural use. To index wetland density, we included wetland edge density (WEDGDEN; km of wetland edge km⁻² of study area; Larivière and Messier 2000). Finally, we created an index of annual wetness (POND) based on wetland counts in May from the nearest three Waterfowl Breeding Population and Habitat Survey segments (WBPHS; US Fish and Wildlife Service and Canadian Wildlife Service 1987). We standardized segment- and year-specific WBPHS wetland counts relative to their long-term (1961–2011) median values and used the inverse distance-weighted value from the nearest three survey segments. Relatively, greater negative and positive POND values represent locally drier and wetter conditions, respectively.

We included within- and among-scale interactions that seemed biologically plausible. At the nest scale, we included an interaction between IDATE and DISTWET (or DISTEDGE), examining potential within-season variation in distance to edge effects. At the patch scale, we included an interaction between HAB and PATCHSZ recognizing that patch size effects may vary with habitat type. At the landscape scale, we included interactions between PCTCROP, PINDEN, and POND, examining the potential for dependencies among these variables. Contingent on the results of within-scale model reductions, we included the among-scale interactions HAB*IDATE, HAB*PCTCROP, HAB*PINDEN and HAB*POND to test whether habitat-specific nest survival varied with season, landscape composition, pintail density or annual moisture.

We standardized IDATE by study site or site-cluster ($\bar{x}=0$, $SD=1$) to account for annual and site effects on this variable. DISTWET, DISTEDGE and PINDEN were square-root transformed, and WEDGDEN was transformed with a natural log, to improve linearity.

We used Akaike's Information Criterion (AIC) adjusted for overdispersion (i.e., Pearson χ^2/df , McCullagh and Nelder 1989; QAIC, Burnham and Anderson 2002) for model selection. Continuous covariates were evaluated as linear or quadratic predictors, and the best fitting form (lowest QAIC) was advanced to full models. We sequentially reduced full models using backward elimination of least predictive covariates (based on P values), while maintaining model hierarchy. P values in this context are used to reflect the percentiles of the reference distributions for the effect F -statistics and thus provide a ranking system for the standardized effect sizes (Perezgonzalez 2015). Where ambiguity occurred between least predictive covariates, each was removed creating parallel model reduction paths. Top models from each scale were combined to create a full multi-scale model which in turn was reduced by backward elimination to arrive at a final model best fitting the data. In all backward elimination procedures, we identified best-approximating models when elimination of additional covariates achieved no further reduction in QAIC (Burnham and Anderson 2002).

Habitat selection analysis

We used resource selection functions (RSFs; Johnson et al. 2006; McLoughlin et al. 2006, 2010) to examine the influence of covariates affecting nest survival on pintail habitat use versus availability. RSFs are useful for inferring selection based on departures from random use, while considering covariate effects that can provide insight into underlying ecological processes (McLoughlin et al. 2010). Given evidence that distance to wetland can affect duckling survival e.g., Rotella and Ratti 1992), we included DISTWET in

habitat selection analysis regardless of its performance in the nest survival analysis.

We used logistic regression (PROC GLIMMIX, SAS Institute; e.g. Gillies et al. 2006) to compare the observed distribution of nest sites among habitats (coded as 1's) with a sample of 300 points (coded as 0's) distributed randomly in ArcMap among all habitat patches searched for waterfowl nests within a study area. Among study areas, random points ($n=270\text{--}292$) and nests were constrained to those located in areas searched at least three times.

Because differences in nest survival rates among habitats can affect the observed number of nests detected (e.g., Peron et al. 2014), we estimated the effects of differing DSR among habitats (from above) on the proportion of nests found given our 3-week nest search interval, and the 32 day laying and incubation period for pintails. The probability of finding a nest given it was active during a search and not previously discovered, was held constant at 0.5 in all habitats. Nest inclusion probabilities were estimated as the likelihood of discovering nests at any age prior to nest destruction or successful hatch. We thus mitigated the effect of DSR on nest detection in each habitat by weighting observed nests by the inverse of the estimated probability of their inclusion in our sample. To account for the clustered data structure, we specified random intercepts at the study area level. Among study areas, 897 pintail nest sites and 17,590 random points were included in the analysis (Online Resource 1).

We began with a full model examining selection ratios among HAB categories and including interactions of HAB with each variable influencing nest survival from the best-fitting nest survival model. Random points were assigned patch and study area level covariate values based on location. We converted IDATE to a categorical variable (IDATE_CAT) for nests and assigned early, mid, and late initiations based on 33rd percentiles of the nest initiation date distribution. We randomly assigned one third of random points to each IDATE_CAT category.

In nest survival and habitat selection analyses, we present and rank models within two AIC units of the best-approximating models. Among ranked models, we considered a model to be a competitor for drawing inference if parameters in a higher ranked model were not simply a subset of those in the competing model. (Burnham and Anderson 2002; Arnold 2010). We used relative AIC weight (w_i) as a measure of support for each model. In all model suites examined, we included a NULL model containing intercept and random effect terms only. We present model-averaged means and effect estimates (± 1 SE) based on top-ranked competing models. We report DSRs and observed nest survival (i.e., proportion of nests that hatch; $=\text{DSR}^{32}$) based on a 32-day average nest age at hatch for pintails (Klett et al. 1986). Habitat selection results are reported as nest:random point selection ratios. The overall nest:random point ratio we

used ($897/17,590=0.051$), provides a general baseline. We infer selection and avoidance of individual habitats based on specific statistical contrasts with a baseline nest:random point ratio estimated for the effect of interest. We report 85% confidence limits for consistency with information theoretic approaches (Burnham and Anderson 2002; Arnold 2010).

Results

Overall, nest searches were conducted on a total of 26,483 ha of habitat (among study area range: 126–2044 ha). Pintail nests comprised 1005 of 9038 nests found; 929 and 897 pintail nests were used in nest survival and habitat selection analyses, respectively. Covariate values varied widely at nest, patch and landscape scales (Table 2).

Nest survival

We examined 50 models relating pintail nest survival to covariates at nest, patch, landscape and multi-scale levels (Online Resource 2). Among multi-scale reduced models, the best-approximating model of nest DSR included HAB, PCTCROP, the quadratic forms of IDATE and POND, and an interaction between PCTCROP and POND ($w_i=0.17$;

Table 2 Untransformed covariate statistics at nest, patch, and landscape scales for pintail nests found at study areas in Alberta and Saskatchewan, 1997–2009

Scale	Covariate	Mean (median*)	Range
Nest ($n=927$)			
	IDATE	136	100–180
	DISTWET (m)	55*	0–444
	DISTEDGE (m)	39*	0–333
Patch ($n=289$)			
	PATCHSZ (ha)	57.3*	0.2–3,158.0
Landscape ($n=62$)			
	PINDEN	23.2*	0–151.7
	DUCKDEN	157.5	27.7–348.5
	WEDGDEN	4.6*	2.5–16.5
	PCTCROP (%)	41.3	0–87.3
	POND	2.4	–0.8–5.2

Covariates: IDATE—days since 1 January (e.g., 135=May 15), DISTWET—distance to nearest wetland edge, DISTEDGE—distance to nearest habitat edge, PATCHSZ—size of habitat patch containing the nest, PINDEN—Pintail pair density (pairs km^{-2} surveyed wetland), DUCKDEN—Non-pintail duck pair density (pairs km^{-2} surveyed wetland), WEDGDEN—wetland edge density (km wetland edge km^{-2} study area), PCTCROP—percent of study area extents in annual croplands, POND—standardized (median absolute deviation [1961–2009]) interpolated May pond count for the year of study from the nearest 3 USFWS/CWS May Breeding Waterfowl Population Survey transects

Table 3). Competing models within two QAIC units included PINDEN replacing PCTCROP and POND covariates, and a simpler form of the best-approximating model including only the linear form of POND. Given relatively low model weights among these models, we model-averaged effect estimates and standard errors (Table 4) but present DSRs as estimated from the highest-ranked model containing each parameter.

The best-approximating model at covariate averages indicated that DSR varied from 0.899 (± 0.024 ; 0.033 nest survival) in wetland margins to 0.959 (± 0.009 ; 0.264 nest survival) in fall-seeded cropland (Fig. 2). DSR exhibited a non-linear relationship with IDATE such that nest survival was highest for mid-season clutch initiations (0.937, ± 0.009 ; 0.125 nest survival; Fig. 2). POND and PCTCROP interacted in this model such that nest survival declined as the amount of cropland increased during dry years, but increased with the amount of cropland in wet years. The amount of cropland had equivocal effects in years of average wetness. A competing model indicated that DSR declined strongly with increasing pintail pair density (Table 3, Fig. 3).

Nest habitat selection

We examined 11 models relating pintail habitat selection to covariates at nest, patch, landscape and multi-scale levels (Online Resource 3). The best-approximating model ($w_i = 0.509$) indicated pintail nest site selection varied from early to late in the nesting season, and depended on the amount of cropland in the surrounding landscape, annual spring moisture, and the pintail breeding pair density with no models competing (Table 5). Fall-seeded crops were avoided early in the nesting season but used as available

Table 4 Coefficient estimates, 85% Confidence Intervals, and index of importance (coefficient of variation [CV]) for covariates predicting daily survival rate of pintail nests ($n=929$) at study areas in Alberta and Saskatchewan, 1997–2009. Model-averaged estimates included coefficients from best-approximating and competing models

Effect	Estimate	85% CI	CV
<i>Model-averaged</i>			
IDATE	– 0.138	– 0.239 to – 0.037	0.503
IDATE ²	– 0.119	– 0.182 to – 0.056	0.369
HAB ^a			
FALCROP	0.852	0.498–1.206	0.289
GRASSIDLE	0.621	0.262–0.980	0.401
PASTURE	0.260	– 0.001–0.521	0.693
HAYLAND	0.484	0.190–0.778	0.421
WETLAND	– 0.186	– 0.671–0.299	1.805
PCTCROP (in PCTCROP*POND models)	– 0.019	– 0.029 to – 0.009	0.352
PCTCROP*POND	0.006	0.003–0.009	0.338
<i>Not model averaged</i>			
PINDEN	– 0.112	– 0.181 to – 0.043	0.427
POND (with POND ²)	– 0.710	– 1.074 to – 0.346	0.356
POND (without POND ²)	– 0.244	– 0.397 to – 0.091	0.436
POND ²	0.082	0.023–0.141	0.506

^aHAB estimates use spring crop as the reference category

thereafter. Throughout the nesting season, idle grasslands were selected for nesting and haylands were used as available. Pasture grasslands were selected early but avoided during mid and late season. Spring-seeded croplands were used as available early and mid-season and avoided late season. Finally, wetland margins were selected nest sites only

Table 3 Best-approximating models (i.e., within two quasi-Akaike Information Criterion [QAIC] units of the top ranked model), full model, and the null model from the multi-scale analysis examining pintail nest survival rate as a function of clutch initiation date (IDATE), habitat type (HAB; Table 1), standardized annual moisture (POND), pintail pair density (PINDEN), non-pintail total duck pair density (DUCKDEN), percent cropland within study areas (PCT-

CROP), and wetland edge density (WEDGDEN) at study areas in Alberta and Saskatchewan, 1997–2009. Competing models (i.e., structurally simpler and/or containing alternate covariates than the top-ranked model; Arnold 2010) within 2 QAIC of the best-approximating model are labeled “Competing”. The NULL model includes only an intercept and random effect term for reference. A full list of models examined is provided in Online Resource 2

Model	QAIC	Parameters ^a	Δ QAIC ^b	Model weight (w_i)
<i>Best approximating:</i> IDATE + IDATE ² + HAB + PCTCROP + POND + POND ² + PCTCROP*POND	1256.9	13	0.0	0.173
<i>Competing 1:</i> IDATE + IDATE ² + HAB + PINDEN	1257.1	10	0.2	0.155
<i>Competing 2:</i> IDATE + IDATE ² + HAB + PCTCROP + POND + PCTCROP*POND	1258.5	12	1.6	0.078
<i>Full:</i> IDATE + IDATE ² + HAB + HAB*IDATE + PINDEN + DUCKDEN + DUCKDEN ² + PCTCROP + WEDGDEN + WEDGDEN ² + POND + POND ² + PCTCROP*POND + PINDEN*POND + HAB*PINDEN + HAB*PCTCROP + HAB*POND	1284.5	39	27.6	0.000
NULL	1272.5	2	15.5	0.000

^aInclude intercept and random effects

^b $n=929$, $c\text{-hat}=1.51$

Fig. 2 Estimated pintail nest survival ($\pm 85\%$ CI) among habitats during early, mid, and late nest initiations at study areas in Alberta and Saskatchewan, 1997–2009. Estimates were derived from the best-approximating model with PCT-CROP, and POND set to mean values (Table 3) and IDATE set to -2.0 (early), -0.5 (mid), and 1.0 (late) for comparison with habitat selection results. Habitat (HAB) acronyms are defined in Table 1

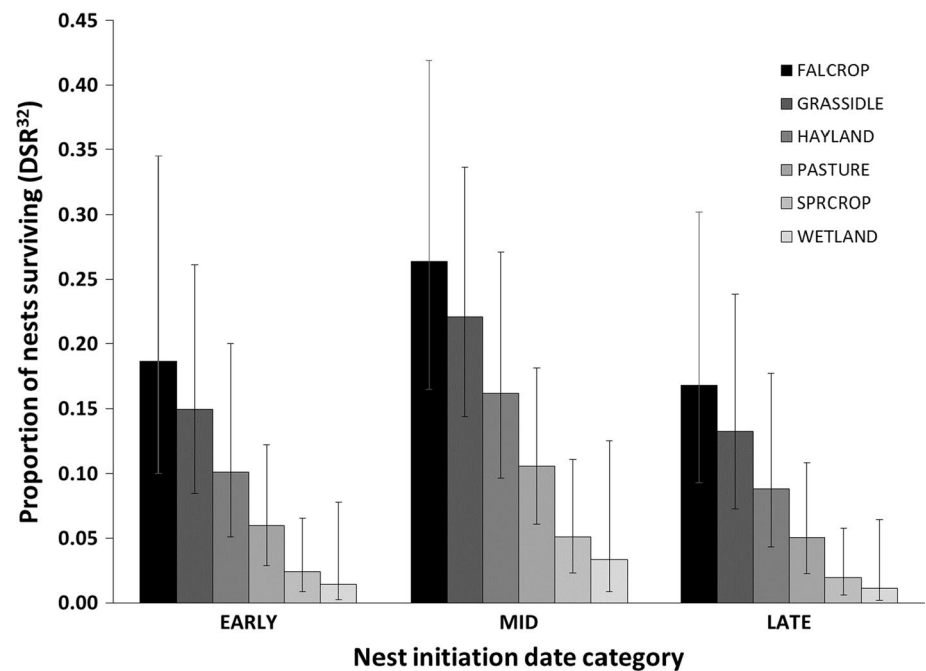
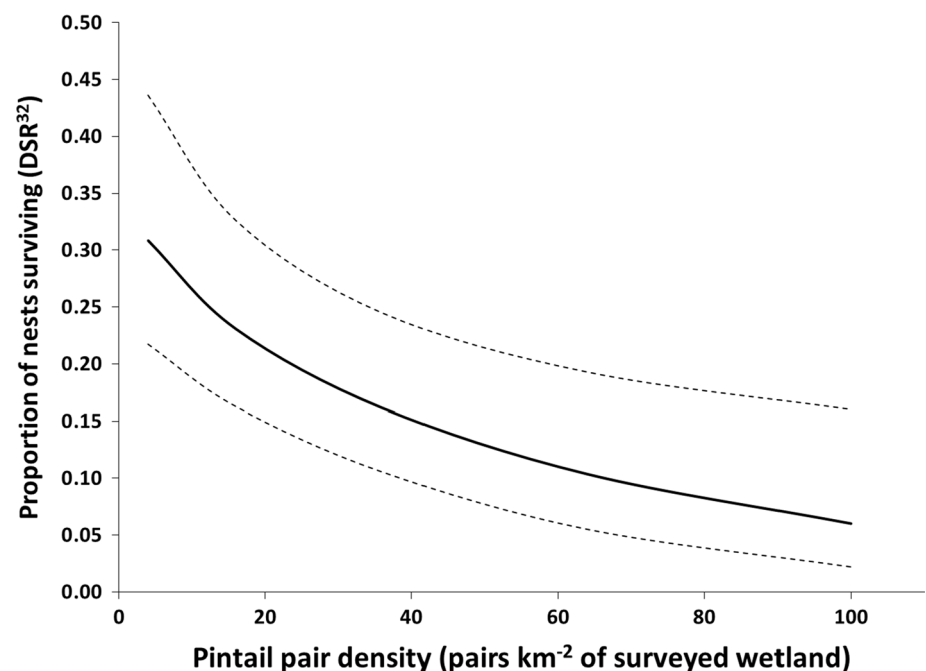


Fig. 3 Estimated pintail nest survival ($\pm 85\%$ CI) in relation to density of pintail pairs (PIN-DEN) at study areas in Alberta and Saskatchewan, 1997–2009. Estimates were derived from the first competing nest survival model (Table 3), averaged across HAB effects and with IDATE set to its mean value



during mid-season and used as available early and late season (Fig. 4). The increase in selection ratios for fall-seeded cropland, and the decline in selection of pasture, were the most notable changes across the nesting season (Fig. 4).

At the landscape scale, nest habitat selection was affected by the amount of cropland, pintail pair density, and annual moisture (Table 5). Selection for idle grassland, and avoidance of spring-seeded cropland and pasture, strengthened as the amount of cropland increased

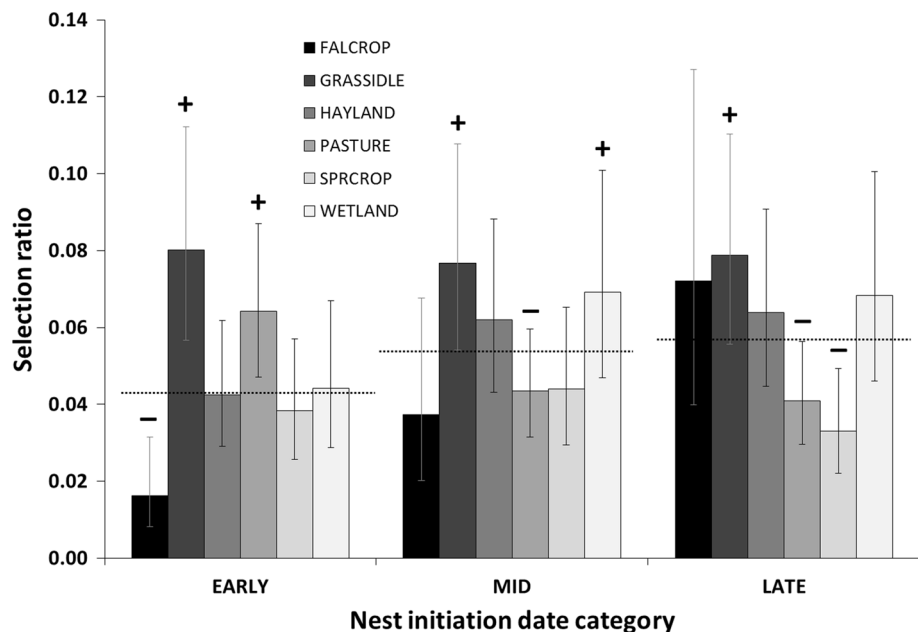
(Fig. 5). Conversely, idle grassland changed from selected to avoided, and spring-seeded cropland changed from avoided to selected, as pintail pair density increased (Fig. 6). Finally, selection of nest sites in idle grassland and hayland was much stronger in wet years, pasture tended to be selected in dry years, and, along with spring-seeded cropland and wetland margins, was avoided in wet years (Fig. 7).

Table 5 Models examining nest habitat preference as a function of variables affecting nest survival at study areas in Alberta and Saskatchewan, 1997–2009. Best-approximating models are those within two Akaike Information Criterion (AIC) units of the top-ranked model. Variables examined include habitat type (HAB; Table 1), a categorical definition of clutch initiation date (IDATE_CAT; representing early, mid, and late initiations), distance to the nearest wetland (DISTWET), pintail pair density (PINDEN), percent cropland

MODEL	Parameters ^a	AIC	ΔAIC	Model weight (w_i)
<i>Best approximating:</i> HAB*IDATE_CAT + HAB*PCTCROP + HAB*PINDEN + HAB*POND + HAB*POND ²	43	13470.0	0	0.509
<i>Full:</i> HAB*IDATE_CAT + HAB*DISTWET + HAB*PCTCROP + HAB*PINDEN + HAB*POND + HAB*POND ² + POND*PCTCROP	49	13472.8	2.8	0.125
NULL	2	13797.8	327.8	0.000

^aInclude intercept and random effects

Fig. 4 Estimated pintail nest habitat selection ratios ($\pm 85\%$ CI) among habitats for early, mid and late clutch initiations at study areas in Alberta and Saskatchewan, 1997–2009. Estimates were derived using the best-approximating model in Table 5, with PCTCROP, PINDEN, and POND set to mean values. Horizontal dashed lines represent the expected selection ratio if habitats were selected in proportion to their availability. Habitats used greater than available (selected) or less than available (avoided) based on statistical contrasts are indicated by + and – symbols, respectively



Discussion

Our analysis provides strong evidence that nest habitat selection by pintails is a highly dynamic process that varies temporally within the breeding season and in response to breeding population density and landscape-level factors. Further, our study demonstrates that habitat selection can exhibit both adaptive and non-adaptive characteristics when viewed from the perspective of a single life history trait responding to many interacting environmental variables. An important assumption in our study was that nest survival is a primary component of pintail fitness, and a driver of nest habitat selection, given the disproportionate

within study areas (PCTCROP), and standardized annual moisture (POND). No competing models to top-ranked models (i.e., structurally simpler and/or containing alternate covariates than the top ranked model; Arnold 2010) were identified. All models with interaction terms include constituent main effects. The NULL model includes intercept and random effect terms for reference. A full list of models examined is provided in Online Resource 3

importance of nest survival versus other vital rates to recruitment potential in many bird species (Ricklefs 1969; Martin 1993; Hoekman et al. 2002). Given the risky nature of terrestrial ground-nesting to attendant females, we recognize other vital rates, like female survival or duckling survival, could impinge on nest site decisions and affect the interpretation of our results (e.g., Devries et al. 2003; Bloom et al. 2012; Chalfoun and Schmidt 2012). Relative to nest survival, the adaptive correspondence of habitat selection was most pronounced late in the nesting season, in highly cropped landscapes, during wet years, and at low population density.

Fall-seeded cropland, with the highest nest survival of any habitat, was avoided early, thereby representing a

Fig. 5 Estimated pintail nest habitat selection ratios ($\pm 85\%$ CI) in landscapes with low, medium, and high percent cropland at study areas in Alberta and Saskatchewan, 1997–2009. Estimates were derived using the best-approximating model in Table 5, with PINDEN and POND set to mean values and applying equal weight across nest initiation date categories. Horizontal dashed lines represent the expected selection ratio if habitats were selected in proportion to their availability. Habitats used greater than available (selected) or less than available (avoided) based on statistical contrasts are indicated by + and – symbols, respectively

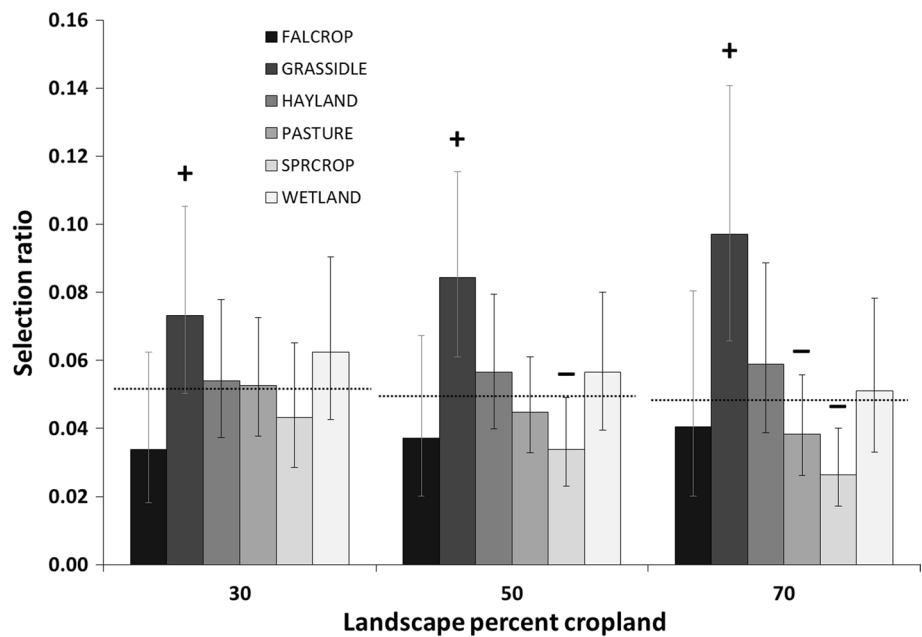
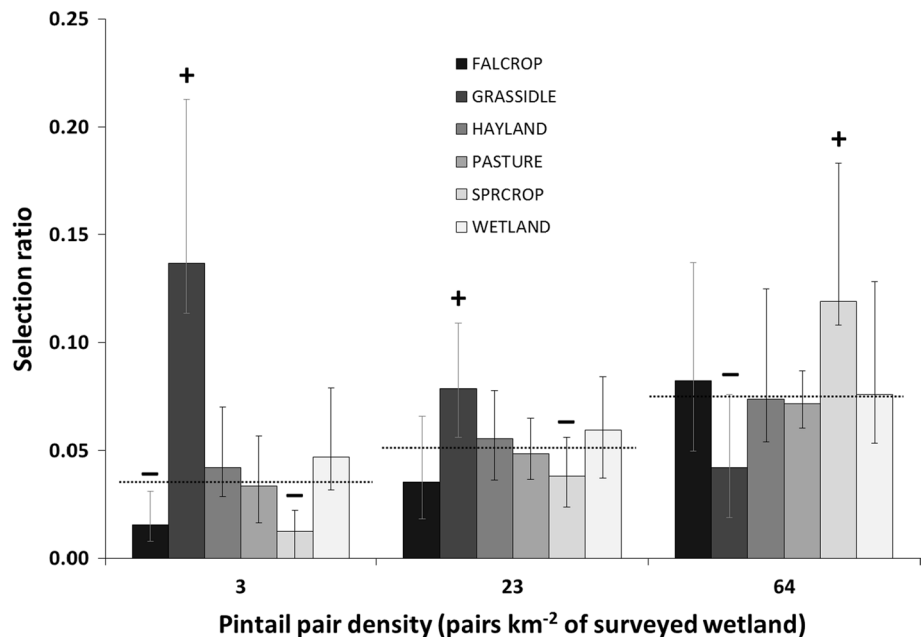


Fig. 6 Estimated pintail nest habitat selection ratios ($\pm 85\%$ CI) in landscapes with low, medium, and high pintail pair density at study areas in Alberta and Saskatchewan, 1997–2009. Estimates were derived using the best-approximating model in Table 5, with PCTCROP and POND set to mean values and applying equal weight across nest initiation date categories. Horizontal dashed lines represent the expected selection ratio if habitats were selected in proportion to their availability. Habitats used greater than available (selected) or less than available (avoided) based on statistical contrasts are indicated by + and – symbols, respectively

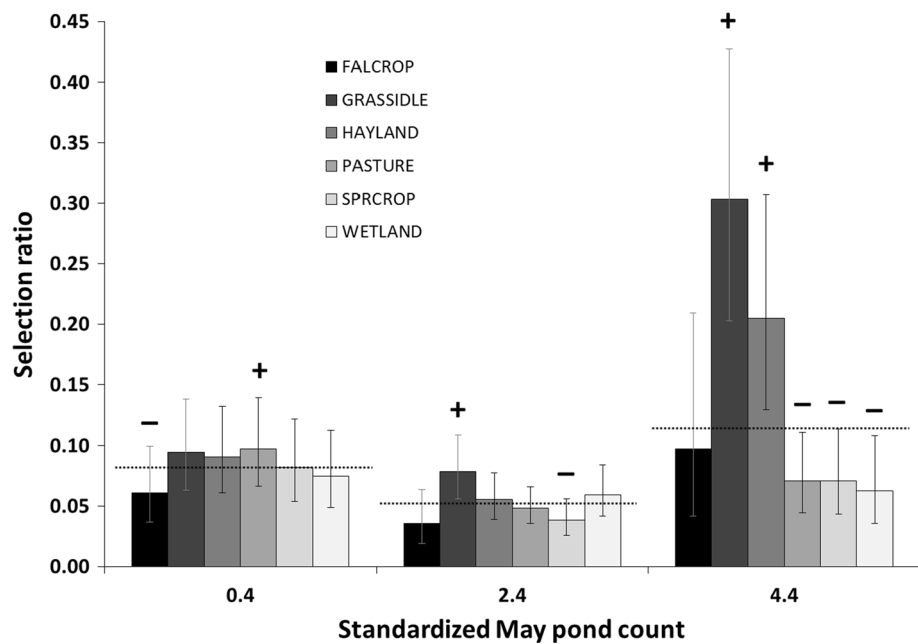


perceptual trap (Patten and Kelly 2010), but relative use rose rapidly through the nesting season. This may be explained in part because fall-seeded crops (winter wheat, fall rye) are relatively rare in prairie Canada and pintails generally would have little experience with them as nesting habitat (e.g., Orians and Wittenberger 1991). However, nest survival in fall crops is likely high given the early provision and rapid development of nest concealment potential during the nesting season unlike spring-seeded cropland—an attribute that may enhance female survival as well (Devries et al. 2003, 2008). Additionally, given that many nests in the late

season population are likely renests following failed nesting attempts, it is plausible that late season patterns reflect a degree of within-season adaptive learning.

Spring-seeded cropland, which had generally low nest survival but was often the most available nesting habitat on our study sites, was used as available except late in the season when it was avoided. Pintails, more than other prairie nesting ducks, often nest in cropland stubble where the risk of anthropogenic disturbance by spring tillage is high (Goeltz 1918; Milonski 1958; Greenwood et al. 1995). Indeed, waterfowl nest survival in croplands is typically very low

Fig. 7 Estimated pintail nest habitat selection ratios ($\pm 85\%$ CI) under dry, average and wet conditions at study areas in Alberta and Saskatchewan, 1997–2009. Estimates were derived using the best-approximating model Table 5, with PCTCROP and PINDEN set to mean values and applying equal weight across nest initiation date categories. Horizontal dashed lines represent the expected selection ratio if habitats were selected in proportion to their availability. Habitats used greater than available (selected) or less than available (avoided) based on statistical contrasts are indicated by + and – symbols, respectively



due to the combined effects of predation and tillage (Higgins 1977; Greenwood et al. 1995; Richkus 2002; this study). In our study, approximately 25% of non-abandonment nest failures in spring-seeded cropland were the result of spring tillage, a result similar to previous estimates (17%, Greenwood et al. 1995; 20–33%, Richkus 2002; 18%, Devries et al. 2008). This has led to the suggestion that spring-seeded cropland may be an ecological trap for pintail breeding in prairie Canada (Miller and Duncan 1999; Richkus 2002). More specifically, this behavior could represent an evolutionary trap if cropland mimics formerly reliable habitat cues that, due to anthropogenic disturbance, are no longer associated with successful reproduction (Schlaepfer et al. 2002). Our results do not support the ecological trap hypothesis at the habitat scale, but suggest that croplands may represent a sink habitat for pintails (Pulliam 1988). A trap may still exist at a landscape rather than habitat scale if pintails across prairie Canada preferentially settle in cropland-dominated landscapes to breed (Devries 2014). For example, Greenwood et al. (1995) estimated 34–45% of pintail nests were initiated in cropland in prairie Canada.

Despite very low nest survival, wetland margins were generally used for nesting as available, were selected during the middle of the nesting season—creating a possible ecological trap, and only avoided during wet years. Low nest survival in this habitat is likely due to high use by foraging predators (Phillips et al. 2003). Thus, selection of nest sites in wetlands may represent a trade-off if, for example, duckling survival is increased due to reduced overland movement from nest to water (e.g., Rotella and Ratti 1992).

Our results indicate that adaptive selection among habitats appeared to strengthen as the amount of cropland

in the landscape increased and during wetter conditions. These patterns were driven by a strengthening of selection for idle grassland, and avoidance of pasture and spring-seeded cropland in highly cropped landscapes and during wetter years, while selection for other habitats changed little. This is a good example, we believe, of a functional response in resource selection (sensu Myerud and Ims 1998) whereby selection of a resource changes with the availability of a dominant habitat (cropland)—indicating a trade-off—possibly in response to changes in predator communities and foraging efficiency as patches of more suitable habitat decrease (e.g., Sargeant et al. 1993; Sovada et al. 2000; Stephens et al. 2005). Likewise, during wetter years when vegetation is more robust, alternate prey more abundant, and nest survival in all habitats is higher (Walker et al. 2013), the benefits of idle grassland selection may be enhanced.

Our results indicate that local population density can have a strong and disruptive influence on adaptive nest habitat selection by pintails. Most strikingly, we observed a switch from adaptive selection at low population density to the emergence of apparently maladaptive selection at high population density. Specifically, selection for idle grassland switched to avoidance (a perceptual trap), and avoidance of spring-seeded cropland switched to selection (a potential ecological trap) at high population density. A broad interpretation of this pattern is that when nest survival in all habitats is low (high population density) the benefits of selection are not as great as when nest survival differentials are high (low population density). It remains possible also that vital rates other than nest survival may drive habitat selection when population density is high.

Density-dependent effects on reproductive success in birds are well established in territorial species with altricial young (e.g., Rodenhouse et al. 2003); however, empirical support is elusive for species with precocial young like waterfowl (e.g., Ackerman et al. 2004). Our findings that pintails experience differing nest survival among habitats, temporal consistency of differences (i.e., no HAB*IDATE interaction), and persistent negative effects of density on nest survival across habitats (i.e., no HAB*PINDE interaction), are contrary to predictions of the ideal-free distribution (Fretwell and Lucas 1969). But whether nest site choice is ‘free’ or ‘ideal’ appears to depend on multiple environmental factors. Our observations are consistent with predictions of density-dependent habitat selection where density may constrain use or availability of habitat (Morris 1987; van Beest et al. 2014), or a preemptive site-dependent mechanism as suggested by Rodenhouse et al. (1997).

Regardless, pintails do not exhibit clear dominance-related hierarchies or behavioral interactions during the process of nest site selection, leaving the putative mechanism somewhat speculative and in need of testing. Female pintails, like other ducks, are subject to intense harassment by paired and unpaired males at high breeding densities (Smith 1968; Derrickson 1978; Titman and Lowther 1975). It is plausible that older females, or females in better condition, are more able to avoid or cope with harassment, and thus occupy high-quality habitat in high density situations. Thus, the ability of female pintails to cope with harassment by males may provide a more plausible explanation than simple dominance as the dispersing mechanism. Use of suboptimal habitat may be accentuated if inexperienced yearling females comprise a greater proportion of the population in years when populations are high.

While understanding adaptive habitat choice is of considerable theoretical interest, application of this knowledge to landscapes, where habitat availability shapes realized fitness outcomes, also is of critical importance for conservation planning (Pulliam 1988, 1996; Beissinger and McCullough 2002; Opdam and Wiens 2002). For nesting northern pintails, use of intensively cropped landscapes is of special interest given the predominance of this habitat throughout much of its core breeding range, where a substantial proportion of the pintail population is exposed to relatively low nest survival. Strategic promotion of fall-seeded crops (winter wheat, fall rye) in landscapes attracting high densities of breeding pintails may benefit pintail populations if successful over broad geographies. Our results also suggest that ongoing efforts to protect remaining grasslands, especially idle grasslands like those in the US Conservation Reserve Program (Reynolds et al. 2001), will benefit the North American pintail population.

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Author contribution statement JHD and RGC conceived and designed the study. JHD conducted the fieldwork, data analysis and wrote the manuscript. LMA provided statistical advice. RGC provided editorial advice.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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