

6-28-2019

# Survival, fidelity, and dispersal of Double-crested Cormorants on two Lake Michigan islands

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Ayers, Christopher R.; Hanson-Dorr, Katie C.; Stromborg, Ken; Arnold, Todd W.; Ivan, Jacob S.; and Dorr, Brian S., "Survival, fidelity, and dispersal of Double-crested Cormorants on two Lake Michigan islands" (2019). *USDA National Wildlife Research Center - Staff Publications*. 2276.

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RESEARCH ARTICLE

## Survival, fidelity, and dispersal of Double-crested Cormorants on two Lake Michigan islands

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Submission Date: August 1, 2018; Editorial Acceptance Date: April 17, 2019; Published 28 June 2019

### ABSTRACT

Colony fidelity and dispersal can have important consequences on the population dynamics of colonial-nesting birds. We studied survival and inter-colony movements of Double-crested Cormorants (*Phalacrocorax auritus*; cormorants) nesting at Spider and Pilot islands, located 9 km apart in western Lake Michigan, during 2008–2014. We used live resighting and dead recovery data from both colonies, plus dead recoveries from throughout North America, in a multistate live and dead encounter model to estimate annual survival, inter-colony movements, plus temporary and permanent emigration to unmonitored sites. Annual survival averaged 0.37 (annual process variation,  $\hat{\sigma} = 0.07$ ) for hatch-year, 0.78 ( $\hat{\sigma} = 0.08$ ) for second-year, and 0.89 ( $\hat{\sigma} = 0.04$ ) for after-second year birds. The best approximating model recognized only 2 age classes for transition probabilities, indicating little difference in fidelity and movement probabilities after the natal year. Annual fidelity to Spider and Pilot islands averaged 0.53 ( $\hat{\sigma} = 0.17$ ) and 0.48 ( $\hat{\sigma} = 0.24$ ) for second-year and 0.55 ( $\hat{\sigma} = 0.23$ ) and 0.62 ( $\hat{\sigma} = 0.16$ ) for after-second year cormorants, respectively, indicating substantial emigration for both age classes. For birds that dispersed, emigration was approximately equally divided among neighboring colonies, temporary emigration sites from which surviving birds subsequently returned, or permanent emigration sites from which birds never returned (but were still encountered through dead recoveries). Our results indicate that Double-crested Cormorants in the Great Lakes have tremendous potential to disperse, which may help to explain their rapid recolonization following historically low populations in the early 1970s.

**Keywords:** colonial waterbird, dispersal, fidelity, Lake Michigan, multistate model, *Phalacrocorax auritus*, survival, temporary emigration

### Survie, fidélité et dispersion de *Phalacrocorax auritus* sur deux îles du lac Michigan

#### RÉSUMÉ

La fidélité à la colonie et la dispersion peuvent avoir des conséquences importantes sur la dynamique des populations d'oiseaux coloniaux. Nous avons étudié la survie et les déplacements inter-colonies de *Phalacrocorax auritus* (cormorans) nichant sur les îles Spider et Pilot, situées à 9 km l'une de l'autre dans la partie ouest du lac Michigan, en 2008–2014. Nous avons utilisé des données de réobservations d'individus vivants et de récupération d'individus morts des deux colonies, en plus des récupérations d'individus morts provenant de l'ensemble de l'Amérique du Nord, dans un modèle multi-états de rencontres d'individus vivants et morts afin d'estimer la survie annuelle, les déplacements inter-colonies, de même que l'émigration temporaire et permanente vers les sites non suivis. La survie annuelle atteignait en moyenne 0,7 (variation annuelle,  $\hat{\sigma} = 0,7$ ) pour les jeunes de l'année (HY), 0,8 ( $\hat{\sigma} = 0,8$ ) pour les jeunes de deuxième année (SY) et 0,9 ( $\hat{\sigma} = 0,4$ ) pour les oiseaux de plus de deux ans (ASY). Le meilleur modèle d'approximation reconnaissait seulement deux classes d'âge pour les probabilités de transition, indiquant peu de différences dans la fidélité et les probabilités de déplacement après l'année de naissance. La fidélité annuelle envers les îles Spider et Pilot était en moyenne de 0,3 ( $\hat{\sigma} = 0,7$ ) et 0,8 ( $\hat{\sigma} = 0,4$ ) pour les SY et 0,5 ( $\hat{\sigma} = 0,3$ ) et 0,2 ( $\hat{\sigma} = 0,6$ ) pour les cormorans ASY, respectivement, indiquant une émigration substantielle pour les deux classes d'âge. Pour les oiseaux qui se sont dispersés, l'émigration était approximativement divisée de façon égale entre les colonies voisines, les sites d'émigration temporaires vers lesquels les oiseaux survivants retournaient subséquemment, ou les sites d'émigration permanents où les oiseaux ne sont jamais retournés (mais étaient encore rencontrés via les oiseaux morts retrouvés). Nos résultats indiquent que *P. auritus* dans les Grands Lacs possède un potentiel de dispersion considérable, ce qui peut contribuer à expliquer la recolonisation rapide après les niveaux de population historiquement bas au début des années 1970.

**Mots-clés:** oiseau aquatique colonial, dispersion, fidélité, lac Michigan, modèle multi-états, *Phalacrocorax auritus*, survie, émigration temporaire

## INTRODUCTION

Colonial nesting occurs in numerous lineages of birds, and is especially common in large-bodied waterbirds such as Sphenisciformes, Procellariiformes, Pelecaniformes, and Ciconiiformes (Lack 1969, Siegel-Causey and Kharitinov 1990). The primary benefits of colonial nesting are believed to include access to limiting nest sites, protection from predators, and proximity to or information about food resources (Siegel-Causey and Kharitinov 1990). But colonial nesting also has recognized costs, including greater levels of competition for food, exposure to diseases and ectoparasites, and intense competition for nest sites (Coulson 2002). If the benefits of nesting at a particular colony outweigh the costs, colonial birds are expected to exhibit site fidelity (natal philopatry and nesting-site fidelity); whereas individuals that incur net costs from nesting in a particular colony are expected to disperse to other colonies, assuming other suitable locations are available (Bried and Vouventin 2002, Coulson and Coulson 2008). Many earlier studies have supposed that colonial waterbirds exhibit high colony fidelity, but as more studies have been conducted that include marked birds from multiple colonies, this perspective has been challenged (Hamer et al. 2001, Coulson 2016).

Studies utilizing returns of marked individuals to a single nesting colony can only measure apparent survival, which represents the product of true survival and fidelity to a particular study colony (te Marvelde et al. 2009). Simultaneous analysis of marked birds from several colonies, using multistate live-encounter models, can estimate dispersal probabilities among monitored colonies (Devlin et al. 2008), and inclusion of “unobservable states” in such models can even allow for estimation of temporary emigration to unmonitored sites (Converse et al. 2009), but apparent survival rates remain confounded by permanent emigration to unmonitored colonies. Joint analysis of live-encounter data with dead recoveries of marked birds recovered throughout their potential range can allow analysts to separately estimate true annual survival, apparent survival to a monitored study area, and annual fidelity to that study area (Barker et al. 2005).

Double-crested Cormorants (*Phalacrocorax auritus*; hereafter cormorants) have rebounded in recent decades from the effects of environmental contaminants and human persecution, and now nest in large numbers throughout much of their historical range (Dorr et al. 2014). Rapid resurgence and recolonization suggest a flexible settling strategy, whereby individuals are willing to disperse and take advantage of new breeding opportunities; however, most research regarding the colony fidelity of Double-crested Cormorants has provided limited inference about dispersal patterns. Duerr et al. (2006) used multistate

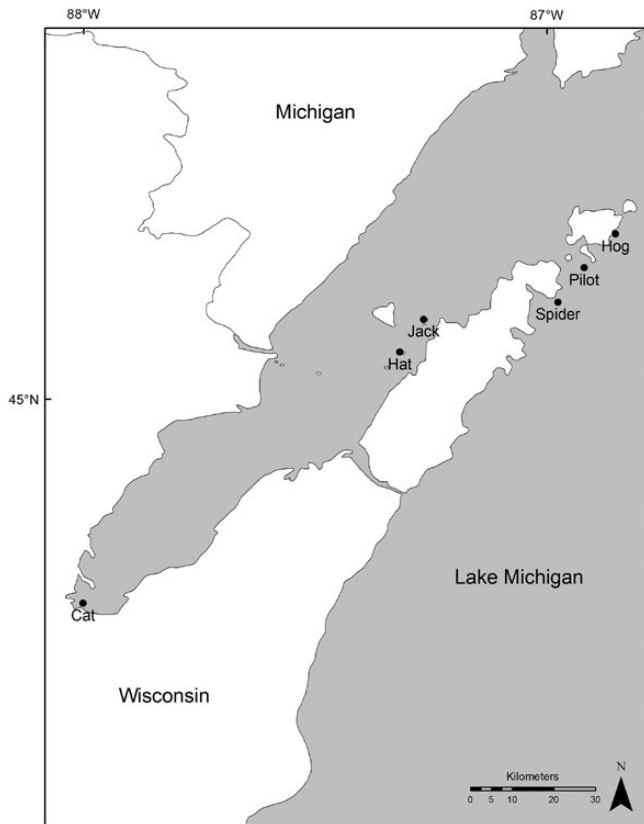
models with live encounters to evaluate movements of nesting adults between a colony subject to varying types and intensity of control efforts and a cluster of uncontrolled colonies located ~35 km apart and found that control effort (egg oiling) increased dispersal from the managed to the unmanaged colonies, but potential emigration to unmonitored sites was not measured. Conversely, Chastant et al. (2014) used joint live-encounter dead-recovery models to evaluate fidelity of cormorants at 2 widely separated (>1,000 km) clusters of colonies and found that 1 cluster exhibited considerable permanent emigration, but temporary emigration and movement among islands within the clusters of colonies were not assessed.

We measured survival, live resighting, and dead recovery probabilities for cormorants from 2 proximate nesting colonies in Lake Michigan, Door County, Wisconsin. Although neither colony was subject to population management, banded cormorants were vulnerable to culling efforts at other managed colonies, and also on their wintering grounds, and hence we obtained a large sample of dead recoveries that enabled us to estimate permanent emigration. In addition, we used multistate models that allowed us to estimate annual colony fidelity, transition probabilities between monitored colonies, and temporary and permanent emigration to unobserved sites. We predicted that younger cormorants would be more likely to exhibit both temporary and permanent emigration from their natal colonies. Better understanding of survival and movements between nesting colonies may help us to better understand the inter-colony dynamics of nesting cormorants, and provide insights for assessing the impacts of population regulation efforts on managed and unmanaged nesting colonies.

## METHODS

### Study Sites

We used mark–resighting–recovery data collected from 2 islands located 9 km apart in Door County, Wisconsin. Spider Island is a 9.2 ha island on the east side of the Door County peninsula in Lake Michigan, and Pilot Island is a 1.5 ha island located 9 km north of Spider Island (Figure 1). Both islands were originally tree-covered, but most living trees died as populations of colonial nesting waterbirds increased, changing soil chemistry with their waste and physically damaging trees (Ayers et al. 2015). Spider Island is part of the U.S. Fish and Wildlife Service (USFWS) Gravel Island National Wildlife Refuge System, whereas Pilot Island is a former working lighthouse with island oversight transferred from the U.S. Coast Guard to the USFWS in 2007 as part of the Green Bay National Wildlife Refuge. Neither of the islands is open to the public and no regular maintenance is performed. Cormorants began nesting on

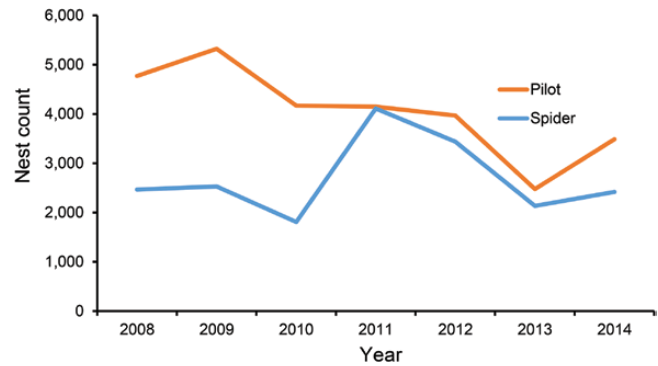


**FIGURE 1.** Map of study area showing Spider Island and Pilot Island (unmanaged cormorant colonies) and Cat, Hat, Jack, and Hog islands (managed colonies) in Lake Michigan near the Door County peninsula of Wisconsin.

Spider Island in the 1970s (Matteson et al. 1999) and on Pilot Island in 1992. From 2008 through 2014, counts of cormorant nests on Spider and Pilot islands fluctuated between 2,000 and 6,000 nests, with nesting populations on Pilot Island exceeding those of Spider Island in all years (Figure 2; S. O'Dell personal communication). Other regional islands that had cormorant nesting colonies previously or during our study and received some level of population management through egg oiling and, to a lesser extent, culling of adults, include Cat, Hat, Jack, and Hog islands (Figure 1).

### Banding and Resighting

We banded ~500 cormorant nestlings in July or August each year on each of Spider and Pilot islands during 2008–2013 (Table 1). In addition, we included data from 29 adults (20 Spider, 9 Pilot) in 2010 and 91 adults (50 Spider, 41 Pilot) in 2011 that we marked as part of a separate study. We marked each bird with an aluminum federal leg band and a unique alpha-numeric plastic leg band (U.S. Geological Survey [USGS] banding permit #22281) that allowed us to identify individuals without recapture. We observed colonies from 2–3 elevated blinds on each island



**FIGURE 2.** Annual nest counts for Double-crested Cormorants on Pilot and Spider islands, Door County, Wisconsin, during 2008–2014.

in June and July 2009–2014 using spotting scopes and binoculars, which provided visibility of all identified nesting areas, although high densities of other nesting birds and downed woody debris limited visibility of small patches on both islands. Most of the birds observed were actively nesting, incubating, and brooding during this time, but we included resightings of all banded birds regardless of behavior or location on the island. However, we excluded 98 observations from 93 birds that were observed on both islands in the same year because we could not reliably identify a breeding colony for these birds. Data from banded cormorants recovered dead were obtained from the USGS Bird Banding Laboratory. We used all band codes indicating recovery of a dead bird, including codes where death was assumed or cause was unknown such as 98 (band only) and 50 (found dead decayed), although these 2 codes were only indicated on ~6% of returns.

### Multistate Modeling

We used Program MARK (White and Burnham 1999) to analyze annual resighting and recovery data in a suite of Burnham joint live (resighting) and dead (recovery) models (Burnham 1993) modified for multiple states (Barker et al. 2005). We recognized 2 observable states (A: Spider Island, B: Pilot Island) and 3 unobservable states (C: temporary emigration from Spider Island, D: temporary emigration from Pilot Island, and E: permanent emigration from either island). Although states A and B were unique geographic locations, states C, D, and E were combinations of geographic locations (i.e. no longer present at Spider or Pilot islands), previous behavior (i.e. emigrated from Spider or Pilot island), and future potential behavior (i.e. C: left Spider but might return, D: left Pilot but might return, or E: left Spider or Pilot with no probability of returning). States C and D were kept separate because they represent separate pools of temporary emigrants that might return someday to their previous colony, whereas permanent emigrants can be combined into a single pool because they will, by definition,

**TABLE 1.** Summary of bandings, live resightings, and dead recoveries of Double-crested Cormorants on Spider Island and Pilot Island, Door County, Wisconsin, 2008–2014. Nest count data from U.S. Fish and Wildlife Service.

Year	Age	Site	Marked	Encountered alive (Pilot Island)										Encountered alive (Spider Island)										Found dead (range-wide)									
				09	10	11	12	13	14	09	10	11	12	13	14	09	10	11	12	13	14	08	09	10	11	12	13	14					
2008	HY	Pilot	395	2	33	29	25	15	13	9	14	6	7	6	3	18	6	2	1	1	1	1	1	1									
2009	HY	Pilot	325	28	29	18	15	15	14	5	7	2	2	6	3	16	5	0	1	2	0	0	0	0									
2010	AHY	Pilot	9	5	2	2	2	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0									
2010	HY	Pilot	529	36	45	23	19	4	19	12	12	12	9	2	9	17	1	7	3	2	2	2	2	2									
2011	AHY	Pilot	41	19	10	4	4	4	4	0	0	0	1	2	2	0	0	0	0	0	0	0	0	0									
2011	HY	Pilot	493	32	40	42	31	39	31	6	12	3	6	12	3	12	5	2	0	0	0	0	0	0									
2012	HY	Pilot	500	31	39	31	39	31	39	2	4	2	4	2	4	24	5	2	0	0	0	0	0	0									
2013	HY	Pilot	500	31	39	31	39	31	39	2	4	2	4	2	4	24	5	2	0	0	0	0	0	0									
Total			2792	2	61	99	141	136	163	9	19	26	27	39	29	18	22	24	14	38	24	11	4	10									
Encounters																								150									
2008	HY	Spider	351	0	5	1	1	2	0	25	44	29	33	21	26	16	8	3	0	0	0	0	0	0									
2009	HY	Spider	486	8	2	7	7	1	1	27	49	33	33	27	25	24	8	3	1	1	1	1	3	3									
2010	AHY	Spider	20	3	1	1	1	1	0	4	4	4	4	2	4	2	2	2	1	0	0	0	0	0									
2010	HY	Spider	450	4	8	4	8	3	3	40	40	33	33	25	31	14	6	1	1	1	1	1	0	0									
2011	AHY	Spider	50	5	2	2	5	2	2	13	11	13	11	8	8	0	0	0	2	1	1	1	1	1									
2011	HY	Spider	499	3	6	9	3	6	9	33	37	31	33	37	31	21	5	1	1	1	1	1	1	1									
2012	HY	Spider	499	4	4	6	4	4	6	16	29	16	29	16	29	14	3	0	2	1	1	1	1	1									
2013	HY	Spider	497	2	2	2	2	2	2	24	24	24	24	24	24	16	3	0	3	0	0	0	0	0									
Total			2852	0	13	10	25	19	23	25	71	122	149	139	178	16	32	27	32	22	24	16	3	8									
Encounters																								161									

HY = hatch year (i.e. juvenile); AHY = after hatch year (adult, age 1+).

never return (i.e. E is an absorbing state). Multistate joint encounter models estimate probabilities of true survival ( $S$ ), live encounter ( $p$ ), transition between states (e.g.,  $\psi_{AB}$ ), and dead reporting ( $r$ ). By recognizing unobservable states (Barker et al. 2005), the model can also be used to estimate temporary emigration ( $\psi_{AC}$ ,  $\psi_{BD}$ ), return immigration ( $\psi_{CA}$ ,  $\psi_{DB}$ ), and permanent emigration ( $\psi_{AE}$ ,  $\psi_{BE}$ ). Although multistate models usually focus on transition probabilities, we were also interested in the probability of birds returning to the island where they were observed the previous year (i.e.  $\psi_{AA}$ ,  $\psi_{BB}$ ; commonly referred to as site fidelity). We estimated these probabilities using multinomial constraints (i.e. the sum of all transition probabilities, including fidelity or non-transition, must equal 1, so  $\psi_{AA} = 1 - \psi_{AB} - \psi_{AC} - \psi_{AE}$ ). We used Program U-CARE to perform a goodness-of-fit test on our data (Choquet et al. 2009), which indicated that birds banded as juveniles were more prone to dispersal ( $\hat{c} = 12.5$ ) than adults ( $\hat{c} = 0.81$ ); we accommodated this lack of fit by considering models with 2 or more age classes when modeling movement probabilities.

We considered models with 1 (all age classes similar), 2 (hatch year [HY] vs. after hatch year [AHY]) or 3 age classes (HY, second year [about one-year-old, SY], and after second year [ $\geq 2$  years old, ASY]) because previous studies have shown that cormorant survival continues to increase with age beyond SY (Stromborg et al. 2012, Chastant et al. 2014). Because SY birds could not be distinguished from ASY at time of banding, all SY birds represented returns or recoveries of birds first marked as HY birds; for models with 3 age classes, we assumed that all of the 120 birds first marked as nesting adults were ASY. We tested 2 age classes vs. 3 age classes because cormorants typically begin nesting after their second year and thus may have different colony fidelity and survival between their second and subsequent years (Weseloh and Ewins 1994, Chastant et al. 2014). We also considered colony-specific variation (i.e. Spider different from Pilot) for all parameters. Because temporary and permanent emigration states (C–E) were unobservable, we set live encounter probabilities for these states equal to zero and assumed that survival and dead recovery probabilities for temporary emigration states were equal to their companion islands (e.g.,  $S_C = S_A$ ,  $S_D = S_B$ ) and that parameters for birds that permanently emigrated equaled those of Spider Island (see Kendall and Nichols 2002). We modeled temporary emigration as transition to unobserved states C or D, and we considered structures where temporary emigration was random by setting the probability of remaining an emigrant equal to emigration rates (i.e.  $\psi_{AC} = 1 - \psi_{CA}$ ,  $\psi_{BD} = 1 - \psi_{DB}$ ). We also considered structures where temporary emigration was nonrandom by separately estimating return immigration rates (e.g.,  $\psi_{AC} \neq \psi_{CA}$ ). We modeled permanent emigration as transition to unobservable state E ( $\psi_{AE}$ ,  $\psi_{BE}$ ), with no possibility of return ( $\psi_{EA}$ ,  $\psi_{EB}$  fixed to zero) to represent birds that emigrate from both islands and

are not re-observed. Models with no temporary or permanent emigration were fit by setting all relevant transition probabilities (i.e. involving C and D, or E, respectively) equal to zero. We used Akaike's Information Criterion adjusted for small sample sizes (AIC<sub>c</sub>) to rank competing models and select best-approximating model(s) for further analysis.

We used the top-ranked model(s) from our assessment of age and site-specific variation to estimate temporal variation in each parameter using the Markov chain Monte Carlo (MCMC) estimator in Program MARK (White et al. 2009). For each time-constant parameter identified in the top-ranked maximum likelihood model, we reconstructed the parameter index matrices in MARK to create fully temporal estimates of that parameter. However, rather than estimate annual parameters as fixed effects, we assigned each original parameter (e.g.,  $S_{HY}$ ) a pair of logit-link hyper-parameters including a mean (e.g.,  $\mu [S_{HY}]$ ) and annual process variation (e.g.,  $\sigma [S_{HY}]$ ), with annual estimates drawn from normal distributions based on these hyper-parameters (e.g., logit ( $S_{HY,t}$ )  $\sim$  Normal( $\mu[S_{HY}]$ ,  $\sigma[S_{HY}]$ ). We then used these hyper-parameter estimates (e.g.,  $\hat{\mu}_{S_{HY}}$ ,  $\hat{\sigma}_{S_{HY}}$ ) to randomly generate 10,000 logit-link parameter estimates and back-transform them to the real parameter scale, where we summarized their mean and standard deviation (SD) to provide estimates of process variation on the real scale. Based on preliminary estimates of necessary sample sizes needed for convergence, we used 2 MCMC chains, including 5,000 iterations for tuning, 20,000 for burn-in, and 15,000 iterations retained to summarize each posterior distribution.

## RESULTS

During 2008–2013, we banded 2,852 cormorants on Spider Island and 2,792 cormorants on Pilot Island (Table 1). For each island, we obtained over 600 resightings from birds that returned to their natal island in subsequent years, and we also obtained 90 resightings of cormorants that moved from Spider to Pilot Island and 149 resightings of birds banded on Pilot Island that moved to Spider Island (Table 1). In addition, we received 161 dead recoveries from birds banded on Spider Island and 150 recoveries from birds banded on Pilot Island. On average, 42% (SD 12.2%) of annual dead recoveries were associated with wildlife management activities (USGS “how obtained” code 44). The second most commonly reported cause of death was unknown cause of death/bird found dead (USGS “how obtained” code 0), an average of 37% (SD 9%) annually. Only 22% of dead recoveries were from Wisconsin (with only 3% from the same islands where marked), 14% were from other Great Lakes states or provinces (e.g., Michigan, USA; Ontario, Canada), 60% were from Gulf Coast wintering areas (e.g., Louisiana, Mississippi, Texas, Alabama, Florida, Mexico), and 4% were from areas between the Great Lakes and Gulf Coast. Dead recoveries came from throughout the

year: 24% during the breeding season (April–August), 33% during fall migration (September–October), and 43% from the winter period (November–March). Hence, we feel confident that dead recoveries are a representative sample of all marked cormorants, including individuals that permanently dispersed from Spider and Pilot islands.

The best approximating maximum likelihood model recognized 3 age classes for survival ( $S_{a3}$ ) and 2 age classes for live-encounter, transition, and dead-recovery probabilities ( $p_{a2}$ ,  $\psi_{a2}$ ,  $r_{a2}$ ). Survival, live-encounter, and dead-recovery probabilities were similar between colonies, but transition probabilities differed between colonies (e.g.,  $\psi_{AB} \neq \psi_{BA}$ ,  $\psi_{AC} \neq \psi_{BD}$ , and  $\psi_{AE} \neq \psi_{BE}$ ); in addition, return immigration was best modeled as nonrandom rather than random, with birds returning to both colonies at greater probabilities than they left ( $\psi_{AC} < \psi_{CA}$ ,  $\psi_{BD} < \psi_{DB}$ ; Table 2). Our top-supported maximum likelihood model was therefore  $S_{a3}, p_{a2}, \psi_{a2 \times s5}, r_{a2}$  (Table 2), and we used this model structure as a template for MCMC modeling to estimate annual process variation.

Convergence diagnostics for the MCMC model were excellent for all real parameters and most beta and hyper-parameters ( $\hat{R} < 1.05$ ), but estimates of permanent emigration rates for adults from Spider Island approached zero, and hence convergence diagnostics for beta- and hyper-parameters for this set of estimates were poor ( $\hat{R} = 1.1 - 1.7$ ). Encounter probabilities were approximately 2 times higher for adults than for juveniles for both live resightings and dead recoveries (Table 3). Annual survival averaged 0.37, 0.78, and 0.89 for HY, SY, and ASY birds, respectively, with moderate amounts of annual process variation ( $\hat{\sigma} = 0.07, 0.08, \text{ and } 0.04$ ; Table 3). Annual colony fidelity averaged 0.48–0.62, with adults exhibiting slightly greater fidelity than juveniles (Figure 3). Temporary and permanent emigration tended to be greater among juveniles, whereas movements between Spider and Pilot islands tended to be greater among adults (Figure 3). Return immigration probability was greater than temporary emigration, with half of all surviving temporary emigrants returning each year, on average (Figure 3).

## DISCUSSION

Survival probability increased with age, but there was no evidence that it differed between colonies. The best supported model for survival indicated that cormorants had low average survival during their first year of life (0.37), with individuals in their second year having somewhat lower survival (0.78) than after-second-year adults (0.89). In addition, measures of annual process variation indicated that survival was more variable for younger age classes and became less variable with age (Table 3). Similar patterns of increasing survival with age for the first 3 to 4 years of life have been observed in other studies of Double-crested

Cormorants (Seamans et al. 2012, Chastant et al. 2014), and in other cormorant species (Catchpole et al. 1998, Hénaux et al. 2007). However, Stromborg et al. (2012) estimated that apparent survival of second- and third-year cormorants (0.774) was greater than that of after-third-year birds (0.633) at Spider Island during 2001–2006, immediately before our study began. Apparent survival measures the proportion of birds that survive and return to their previous colony, so it is possible that adults from Spider Island had lower colony fidelity, or perhaps greater breeding-season mortality, during 2001–2006.

Average annual survival for ASY adults from our study (0.89) was similar to earlier studies that estimated true survival of Double-crested Cormorants based on range-wide band recoveries (e.g., 0.88, Seamans et al. [2012]; 0.83–0.87, Chastant et al. [2014]), whereas our estimate of average annual HY survival (0.37) was intermediate to estimates from these 2 studies (range: 0.19–0.45). Our results suggest that culling efforts that took place during our study on the wintering grounds and on neighboring nesting islands within the Great Lakes had limited impact on overall survival rates at these 2 colonies.

Live-resighting probability was much lower after the first year of life (0.34; i.e. when surviving HY cormorants returned to the colonies as SY birds) than for subsequent years, when ASY cormorants were resighted with a 0.63 probability. Similar results were obtained in an earlier study on Spider Island, where returning SY birds had 0.205 resighting probability vs. >0.55 probabilities for older adults (Stromborg et al. 2012). Given that SY and ASY should be equally observable if they were nesting on Spider or Pilot islands, we interpret the lower resighting probabilities for SY vs. ASY birds as evidence of lower breeding propensity by SY birds (Blums et al. 1996). We recommend that future researchers consider adopting multiple secondary encounter periods per nesting season (i.e. Barker robust-design models; Kendall et al. 2013) so that resighting failure can be differentiated from deferred recruitment.

We observed lower probabilities of colony fidelity (0.48–0.62) than in other studies, but definitions of sites have varied considerably among studies. Cormorants nesting at Lake of the Woods, Ontario, had 0.68–0.80 annual fidelity, and birds nesting in eastern Lake Ontario exhibited 0.94 colony fidelity (Chastant et al. 2014), but in both of these cases sites were defined as clusters of nesting islands rather than a single colony (4 colonies, 0.4–1.6 km apart, and 3 colonies, 3.8–17.0 km apart, respectively). Duerr et al. (2006: their table 5) reported dispersal rates for cormorants nesting at Lake Champlain, New York, from which we estimated colony-specific fidelity rates of 0.50 to 0.96, but part of their definition of dispersal included within-island movements due to egg-oiling activities. In addition, our estimate of colony fidelity accounts for both temporary and permanent emigration to unmonitored



**TABLE 2.** Summary of sequential model-selection decisions to identify appropriate model structures for subsequent analysis of annual survival ( $S$ ), live encounter ( $p$ ), inter-colony transition ( $\psi_t$ ), temporary emigration ( $\psi_i$ ), re-immigration ( $\psi_r$ ), permanent emigration ( $\psi_p$ ), and dead reporting probabilities ( $r$ ) of Double-crested Cormorants banded on Spider and Pilot Islands, Door County, Wisconsin, 2008–2014. Stage 1 identifies an appropriate number of age classes for each parameter ( $a\#$ , where  $a1$ : all age classes similar,  $a2$ :  $HY \neq AHY$ , and  $a3$ :  $HY \neq SY \neq ASY$ ). Stage 2 considers site-level ( $s$ ) variation (i.e. whether parameters differ between Spider and Pilot Islands). Stage 3 identifies appropriate emigration structures, including presence/absence of temporary or permanent emigration (parameters fixed to 0), and models where return immigration equals ( $\psi_t = \psi_i$ ) or does not equal re-immigration. At each stage, the best-supported (lowest  $AIC_c$ ) model is highlighted by bold text:  $k$  is number of parameters.

$S$	$p$	$\psi_i$	$\psi_t$	$\psi_r$	$\psi_p$	$r$	$\Delta AIC_c$	$k$	$-2\log(L)$
Stage 1: Assess age structure in all parameters									
a1	a1	a1	0	0	0	a1	973.7	4	14,335.9
a2	a2	a2	0	0	0	a2	88.3	8	13,442.5
a3	a3	a3	0	0	0	a3	78.1	12	13,424.2
<b>a3</b>	<b>a2</b>	<b>a2</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>a2</b>	<b>72.6</b>	<b>9</b>	<b>13,424.7</b>
Stage 2: Assess site-level ( $s$ ) variation (between islands)									
a3*s	a2*s	a2*s	0	0	0	a2*s	74.8	18	13,408.9
a3	a2*s	a2*s	0	0	0	a2*s	73.6	15	13,413.7
a3*s	a2	a2*s	0	0	0	a2*s	71.9	16	13,410.0
a3*s	a2*s	a2	0	0	0	a2*s	77.5	16	13,415.6
a3*s	a2*s	a2*s	0	0	0	a2	72.7	16	13,410.8
<b>a3</b>	<b>a2</b>	<b>a2*s</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>a2</b>	<b>66.9</b>	<b>11</b>	<b>13,415.1</b>
Stage 3: Add temporary and permanent emigration									
<b>a3</b>	<b>a2</b>	<b>a2*s</b>	<b>a2*s</b>	<b>s</b>	<b>a2*s</b>	<b>a2</b>	<b>0.0</b>	<b>21</b>	<b>13,328.1</b>
a3	a2	a2*s	a2*s	= $\psi_t$	a2*s	a2	3.6	19	13,335.6
a3	a2	a2*s	a2*s	s	0	a2	6.3	17	13,342.4
a3	a2	a2*s	0	0	a2*s	a2	45.5	15	13,385.6
Stage 4: Add temporal variation ( $t$ ) to all parameters for Markov chain Monte Carlo models									
a3*t	a2*t	a2*s*t	a2*s*t	s*t	a2*s*t	a2*s*t	79.5	142	13,159.9

**TABLE 3.** Annual parameter estimates and standard deviations (SD) from a multistate Burnham joint live–dead model including annual survival (S), live encounter (p), dead recovery (r), and transition (ψ) probabilities between 2 observable states (A: Spider Island, B: Pilot Island) and 3 unobservable states (C: temporary emigration from Spider Island, D: temporary emigration from Pilot Island, and E: permanent emigration from either island) for Double-crested Cormorants nesting on Spider Island and Pilot Island, Door County, Wisconsin, 2008–2014.

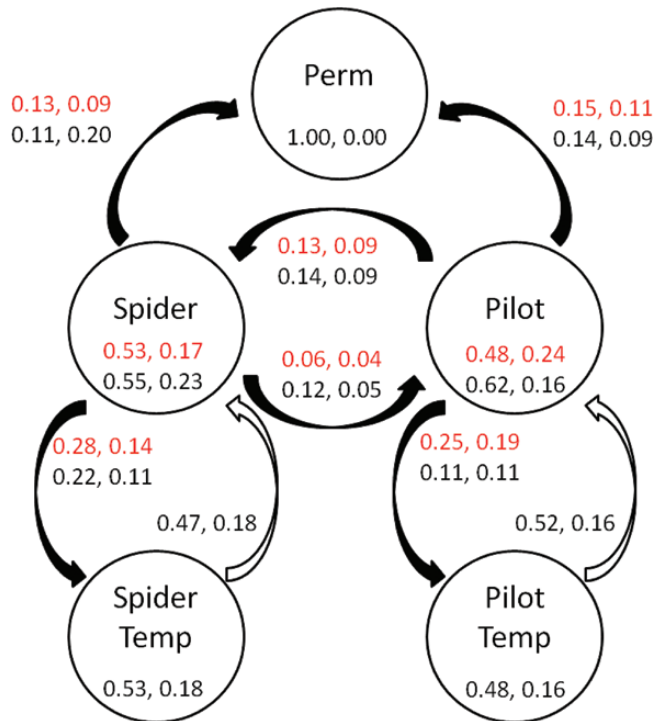
Parameter	Age <sup>a</sup>	2008	SD <sup>b</sup>	2009	SD	2010	SD	2011	SD	2012	SD	2013	SD	2014	SD	μ <sup>c</sup>	σ
S	HY	0.39	0.05	0.38	0.05	0.37	0.05	0.38	0.05	0.33	0.05	0.35	0.05	0.07	0.07	0.37	0.07
S	SY			0.76	0.06	0.75	0.07	0.78	0.06	0.82	0.05	0.78	0.05	0.07	0.07	0.78	0.08
S	ASY					0.88	0.04	0.89	0.04	0.89	0.04	0.89	0.04	0.04	0.04	0.89	0.04
p	SY			0.28	0.05	0.39	0.07	0.39	0.05	0.34	0.05	0.30	0.05	0.31	0.08	0.34	0.09
p	ASY					0.72	0.07	0.67	0.07	0.64	0.05	0.56	0.05	0.58	0.07	0.63	0.11
r	HY		0.07	0.07	0.01	0.05	0.01	0.06	0.01	0.06	0.01	0.05	0.01	0.06	0.03	0.06	0.02
r	AHY			0.19	0.07	0.18	0.07	0.12	0.05	0.15	0.06	0.14	0.06	0.12	0.05	0.15	0.06
ψAB	SY			0.04	0.02	0.08	0.03	0.06	0.02	0.06	0.02	0.08	0.02	0.03	0.03	0.06	0.04
ψAB	ASY					0.12	0.03	0.13	0.03	0.13	0.03	0.10	0.02	0.12	0.03	0.12	0.05
ψAC	SY			0.24	0.11	0.36	0.12	0.20	0.10	0.26	0.11	0.33	0.14	0.14	0.14	0.28	0.14
ψAC	ASY					0.18	0.08	0.27	0.08	0.24	0.07	0.22	0.08	0.20	0.09	0.22	0.11
ψAE	SY			0.11	0.09	0.14	0.10	0.15	0.10	0.15	0.11	0.19	0.13	0.03	0.04	0.13	0.09
ψAE	ASY					0.03	0.04	0.02	0.03	0.03	0.04	0.03	0.04	0.03	0.04	0.11	0.20
ψBA	SY			0.21	0.06	0.10	0.03	0.15	0.04	0.08	0.03	0.06	0.03	0.03	0.03	0.13	0.08
ψBA	ASY					0.18	0.15	0.11	0.04	0.10	0.03	0.19	0.04	0.09	0.03	0.14	0.09
ψBD	SY			0.50	0.10	0.16	0.10	0.16	0.09	0.29	0.11	0.17	0.11	0.11	0.10	0.25	0.19
ψBD	ASY					0.15	0.19	0.13	0.10	0.09	0.08	0.09	0.08	0.08	0.11	0.11	0.11
ψBE	SY			0.19	0.11	0.16	0.09	0.18	0.10	0.13	0.09	0.14	0.10	0.10	0.10	0.15	0.12
ψBE	ASY					0.15	0.12	0.17	0.09	0.14	0.07	0.14	0.07	0.15	0.09	0.14	0.09
ψCA	ASY					0.52	0.19	0.58	0.16	0.45	0.14	0.36	0.13	0.47	0.15	0.47	0.18
ψDB	ASY					0.60	0.14	0.47	0.20	0.51	0.20	0.48	0.20	0.52	0.21	0.52	0.16

<sup>a</sup>HY = hatch year (i.e. juvenile), SY = second year (yearling), AHY = after hatch year (adult, age 1+), or ASY = after second year (adult, age 2+).

<sup>b</sup>Standard deviations based on 15,000 posterior samples obtained via Markov chain Monte Carlo (MCMC) sampling using the MCMC sampler in Program MARK.

<sup>c</sup>Annual mean (μ) and process variation (σ) based on 10,000 back-transformed parameter estimates simulated using the hyper-parameter estimates obtained from our MCMC analysis in Program MARK.

<sup>d</sup>Permanent emigration of adults from Spider Island was poorly estimated (hyper-parameters: mean = -4.24, SD = 6.15 on the logit scale). When back-transformed to the real scale, this led to a highly right-skewed distribution on the real scale, hence μ exceeds the average of all observed values.



**FIGURE 3.** Estimates of average transition probabilities and their annual process variation ( $\hat{\psi}$ ,  $\hat{\sigma}_{\psi,t}$ ) for juvenile (red text) and adult (black text) Double-crested Cormorants remaining in the same state (estimates inside the circles), emigrating from Spider or Pilot islands to other states (solid arrows), or returning from temporary emigration states (open arrows from Spider Temp or Pilot Temp). Permanent emigration (Perm) is an absorbing state with zero probability of return, and all birds reach adulthood before they can re-immigrate from temporary emigration states (hence the absence of juvenile re-immigration probabilities). Note that transition probabilities sum to 1 (e.g., surviving juveniles from Spider Island can remain at Spider 0.53, disperse to Pilot 0.06, temporarily emigrate to Spider Temp 0.28, or permanently emigrate 0.13, with  $0.53 + 0.06 + 0.28 + 0.13 = 1$ ). Parameter estimates were based on 10,000 Monte Carlo simulations derived from hyper-parameters obtained in a multistate Burnham joint live–dead encounter analysis conducted using Markov chain Monte Carlo procedures in Program MARK.

sites, whereas [Chastant et al. \(2014\)](#) accounted for permanent but not temporary emigration to unmonitored sites, and [Duerr et al. \(2006\)](#) accounted for neither. Our study design was most similar to [Hénaux et al. \(2007\)](#), who studied 6 colonies of nesting Great Cormorants in Denmark. Their analysis included unobservable temporary emigration states (attributed to nonbreeding) for each colony, as well as a permanent emigration state observable only through dead recoveries. In their analysis, colony fidelity ranged from 0.27 to 0.94 for Great Cormorants marked as chicks, and from 0.83 to 0.87 for birds that had been observed previously as breeding adults ([Hénaux et al. 2007](#), their [tables 3 and 4](#)). Studies of other Great Cormorant and Shag colonies in Europe indicate even greater levels of colony

fidelity ([Aebischer 1995](#), [Frederiksen and Bregnballe 2000](#), [Coulson 2016](#)).

By simultaneously monitoring 2 colonies, and including range-wide dead recovery data, we were able to estimate movements between Spider and Pilot islands, to temporary emigration states from which surviving cormorants could someday return, and to permanent emigration states from which return emigration was zero. Estimates of natal dispersal by HY birds were typically greater than estimates of breeding dispersal by AHY birds ([Figure 3](#)), and these differences were largest for temporary emigration. Temporary emigration by young birds might represent greater probability of nonbreeding, exploring the greater landscape for other nesting opportunities, or choosing not to migrate back from wintering areas for their first breeding season ([King et al. 2012](#)). The high probability of return-immigration ( $\sim 0.5$ ) suggests that many temporary emigrants could represent birds that become nonbreeders for a single breeding season, perhaps due to high competition for nesting sites on our study colonies.

Our results showing high rates of natal and breeding dispersal between monitored and unmonitored colonies suggest that the willingness of individuals to leave established colonies and pioneer into new locations may be an important driver of recent range and population expansion in Double-crested Cormorants ([Dorr et al. 2014](#)). These patterns suggest enormous potential for Double-crested Cormorants to repopulate, recolonize, and establish new colonies in North America.

## ACKNOWLEDGMENTS

We acknowledge the help of USDA Wildlife Services, West Virginia University, and USFWS staff with data collection. Brett Sandercock, Bret Collier, and an anonymous reviewer provided helpful reviews on earlier drafts of the manuscript.

**Funding statement:** Funding was provided by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services and the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Cooperative Agreements #14-7428-1030-CA, #15-7428-1030-CA.

**Ethics statement:** Use of avian subjects was approved by the USDA, WS, National Wildlife Research Center's Institutional Animal Care and Use Committee (QA-1980).

**Author contributions:** B.S.D., K.C.H.-D., and K.S. conceived the idea, design, or experiment (supervised research, formulated question or hypothesis). K.S., K.C.H.-D., B.S.D., and C.R.A. performed the experiments (collected data, conducted the research). C.R.A., T.W.A., K.C.H.-D., and B.S.D. wrote the paper. K.S., K.C.H.-D., B.S.D., T.W.A., and J.S.I. developed or designed methods. C.R.A. and T.W.A. analyzed the data. K.S. and B.S.D. contributed substantial materials, resources, or funding.

**Data availability:** All data for bird banding and band observation are archived with U.S. Department of Agriculture,

Wildlife Services, National Wildlife Research Center under QA-1980 and are available on request. [https://www.aphis.usda.gov/aphis/ourfocus/wildlifedamage/programs/nwrc/sa\\_information\\_services/ct\\_archives](https://www.aphis.usda.gov/aphis/ourfocus/wildlifedamage/programs/nwrc/sa_information_services/ct_archives)

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