



A group movement model for waterfowl aggregation

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Abstract

This paper presents a simple stochastic model of the dynamics of waterfowl aggregation, investigates model fit, and considers variance in the model's parameter estimators. The model, a marked-point process with four parameters, describes a behavioral process defined by the movements of animal groups. My approach provides new methods to explore animal social behavior. I illustrate the fit of the model to field observations of 39 aggregations observed when they were not at equilibrium and outline a procedure for determining which parameters, and hence which behaviors, are constant across the 39 aggregations. A comparison of the predicted variability in the model's parameter estimates, assuming constant parameter values for all 39 aggregations, to the observed variability in the estimates suggests that waterfowl aggregation dynamics are affected by changing movement rates and not changes in group size: simulations reveal that the estimates of the arrival and departure rates are more variable than expected. In contrast, the estimates of the parameters describing movement group size do not show excessive variability. The fit of a constant parameter modified-geometric distribution to the group size data indicates that the formation of movement groups is not a complicated process. Analysis of the extra variability in the movement rates reveals two variables, migratory season and overall waterfowl density, that influence the behavior of aggregating birds.

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1. Introduction

Because direct observation of individual interactions is difficult for many species, conspicuous animal aggregations, such as flocks of foraging birds, provide data critical to the study of social behavior (Bushkirk, 1976; Morse, 1977; Bertram, 1978; Pulliam and Caraco, 1984; Barnard and Thompson, 1985). Theoretical approaches to model animal aggregations have included spatio-temporal models, such as 'Eulerian' partial differential equations (e.g., Okubo, 1980, 1986; Britton, 1989; Gueron and Liron, 1989) and 'Lagrangian' individual-based equations of

motion and velocity (e.g., Warburton and Lazarus, 1991; Romey, 1996; Flierl et al., 1999), as well as cellular automaton models (e.g., Stöcker, 1999). Group-size distribution models describing fission–fusion processes (e.g., Morgan, 1976; Okubo, 1986; Gueron and Levin, 1995; Duerr and Dietz, 2000) and a rich variety of game-theoretic, probability, and dynamic optimization models have also supplied clues to the causes of gregariousness (Thompson et al., 1974; Rubenstein, 1978; Clark and Mangel, 1984, 1986; Clark, 1987; Mangel, 1990; Rasa, 1990; Szekely et al., 1991; Giraldeau and Caraco, 2000; Hamilton, 2000). While these models are motivated by observation of animal behavior, few efforts to connect models directly to empirical data on aggregation have been attempted (but see, e.g., Okubo, 1986; Turchin,

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1989; Turchin and Simmons, 1997). Better connection between models and data is the necessary next step in understanding grouping behavior (Parrish and Edelstein-Keshet, 1999). Due to the difficulty of observing and recording dynamic aggregative behavior, data driven models are typically simple, Markovian descriptions of behavior that emphasize equilibrium conditions (e.g., Cohen, 1969, 1971, 1972, 1975; Caraco, 1980; Wood, 1985). Quenette et al. (1997) used a model similar to the one presented here to describe the behavior of a small number of captive snowshoe hares (*Lepus americanus*). This paper presents an empirically motivated, Markovian aggregation model that extends these previous approaches by considering variable-sized movement groups. Moreover, my approach does not assume equilibrium conditions, but does depend on observation of aggregation dynamics.

I model field observations of the formation of mixed-species waterfowl aggregations as a stochastic process characterized by frequent arrivals and departures of groups of birds. The data I collected are unusual because I observed (1) the initiation and formation of aggregations, (2) the size of movement groups, and (3) the size of the pool of aggregating individuals. The aggregations I recorded did not reach equilibrium, and, given the long time scale of the process, they were unlikely to ever do so. The total number of waterfowl present and the composition of the community also changed substantially between aggregation observations. Despite these changes, I present a parsimonious model that describes the independent movement groups and includes no species-specific behavior. Starting with a simple neutral model is appropriate here, because it allows me to identify a small number of critical parameters describing a complex behavioral process. Similar models have been used to describe single species aggregations (Cohen, 1969, 1971, 1972, 1975; Caraco, 1980; Wood, 1985; Quenette et al., 1997), but have not been applied to mixed-species aggregations.

The model is a continuous-time, discrete-state Markov process with four parameters. The sources of stochasticity are the timing of movements and the number of birds that arrive or depart during each move. The inclusion of variable-sized movement groups is a critical component, incorporated because an earlier model highlighted the importance of associations among birds during movement (Silverman

et al., 2001). Previous Markov aggregation models have not included the movement of groups, and most stepping-stone type models do not allow simultaneous movements of multiple individuals (Renshaw, 1986), in part because such formulations significantly complicate analysis. Wood (1985), for example, treated paired birds as singletons. Models of population processes with catastrophic events (Brockwell et al., 1982; Hastings, 1995) and branching models that include group migration (Pakes, 1986) are exceptions to this general rule. The model presented here is another exception. Since many animals migrate and move in social and family groups, aggregation formation resulting from group movements is not restricted to waterfowl. For example, Baird and Dill (1996) describe short term associations among killer whales *Orcinus orca* that form when members of different pods join together to hunt. Jarman's (1974) classification of African antelope social organization includes species in which small groups aggregate into large herds during migration. Colonial nesting birds are known to follow one another on foraging trips (Emlen and Demong, 1975; Evans, 1982; Evans and Welham, 1985; Brown and Brown, 1996). Thus, models that incorporate group movements should have wide applicability.

After confirming model fit, I develop an approach for identifying the model parameters that should be analyzed in relation to exogenous variables. Simple Markov models of aggregation dynamics, such as the one I present, are most useful when their parameter values can be related to ecological factors (Pulliam and Caraco, 1984). For example, Caraco (1980) compared estimated movement rates of yellow-eyed juncos *Junco phaeonotus* among different food densities and temperatures to support his predictions about the relationship between these variables, aggression, and flock size. In contrast, similar models of avian aggregations and primate social groups (Cohen, 1969, 1971, 1975; Wood, 1985) have drawn conclusions about the factors affecting social dynamics from an evaluation of model fit: situations in which the model fit were compared to those in which the model failed.

I suggest calculations that identify parameters for further analysis, when model fit is good. In order to detect real patterns in sets of parameter estimates, it is necessary to first quantify the variance of the

estimators under a constant-parameter model (see, e.g., Bart et al., 1998 for a brief description of methods for variance estimation and approximation); parameters with estimated values outside the expected range are candidates for comparison to ecological variables. Quantifying expected estimator variation is also valuable for determining the robustness of model predictions. Wood (1985) determined that the fit of a model of common merganser *Mergus merganser* aggregation was insensitive to substantial changes in parameter values, but did not distinguish regions of likely and unlikely parameter values. In general, methods that account for natural variation when considering patterns in parameter estimates are lacking, despite their potential utility (Link, 1999).

In the following section, I explain the model and then detail data collection from a series of 39 aggregation formation observations. After presenting the statistical methods and a description of model simulations, I demonstrate the model's fit, using parameters estimated independently for each aggregation. I next employ model simulations to explore whether the 39 sets of parameter estimates are more variable than expected if all the aggregations were generated from a common set of underlying parameter values. This procedure allows me to determine which behavioral parameters changed significantly during the course of data collection. To better understand the aggregative behavior of waterfowl, I consider several explanations for extra variability in the estimates of movement rates: day of observation, season, time in season, disturbance, and waterfowl density. Migratory season and waterfowl density appear to be the most important factors affecting movement into the aggregations.

The model presented here provides a simple description of a complex behavioral process and depends on a small number of measurable parameters. The inclusion of group movements and consideration of non-equilibrium conditions extends my work beyond similar models. I show how to test model fit and explore how the aggregation process varies with several independent variables. This work illustrates methods to connect empirical observations to behavioral models and to quantify and explain parameters important to animal aggregation.

2. Methods

2.1. Aggregation model

The model, a marked-point process, describes a closed, two-colony immigration–emigration system (Whittle, 1967; Renshaw, 1986) defined by the following quantities. The number of birds in the aggregation at time t , $N(t)$, is a random variable. The total number of birds present in the system and available to join the aggregation, B , is constant. The probability a bird decides to depart the aggregation during any small time interval is proportional to the length of the interval and the probability of more than one departure event in this small time interval is negligible. If $r_d h$ is the probability a bird decides to depart in the interval h and $N(t) = n$ birds are in the aggregation, then the probability of a departure in the interval $(t, t + h]$ is, to lowest order, $r_d n h$. Similarly, the probability a bird decides to move into the aggregation during an interval of length h is proportional to h and only one decision to join is made during the interval. Given $r_a h$ is the probability a single bird decides to join, then the probability of arrival is, to lowest order, $r_a (B - n) h$. For these assumptions, the time interval between successive arrival and departure decisions has an exponential distribution with rate $\lambda = r_a (B - n) + r_d n$ (Taylor and Karlin, 1984).

The movement of an individual bird can trigger the movement of additional birds. Specifically, I assume that the movement group size, G , has a modified-geometric distribution with

$$\begin{aligned} \Pr(G = k) &\equiv g_k \\ &= \begin{cases} (1 - \gamma_1), & \text{for } k = 1, \\ \gamma_1 \cdot \gamma_2 (1 - \gamma_2)^{k-2}, & \text{for } k = 2, 3, 4, \dots, \end{cases} \end{aligned} \quad (1)$$

where γ_1 is the probability of a multi-bird group and the number of additional birds has a geometric distribution with parameter γ_2 . Fig. 1 illustrates the distribution for typical waterfowl aggregation parameter values. High values of γ_1 indicate many multi-bird movements. When $\gamma_1 = 0$, all birds move alone and act independently. Previous analysis rejected the model with $\gamma_1 = 0$ (Silverman et al., 2001). When $\gamma_2 = 1$ all multiple bird groups are pairs, while low values of γ_2 indicate many large groups and relatively fewer pairs.

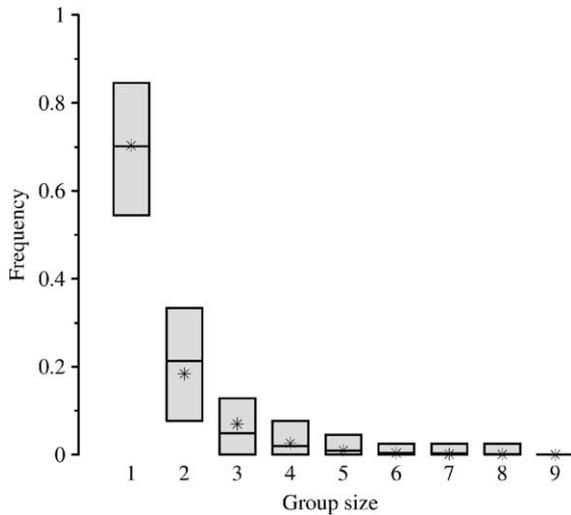


Fig. 1. The estimated group size distribution based on 250 random samples of size 39 with one group chosen from each aggregation's observed group sizes. The central horizontal line through the shaded box is the mean proportion for the 250 random samples. The bottom of the box indicates the 5th percentile and the top of the box indicates the 95th percentile. The stars denote the proportion predicted by the modified-geometric distribution, using the parameters estimated from the combined group sizes (Table 2). The last bin represents all groups greater than eight birds.

The distribution assures that the majority of multi-bird groups are pairs. This is a reasonable constraint, since many species of waterfowl form pair bonds during the fall and winter, and females benefit from male attendance (Paulus, 1983; Hepp and Hair, 1984; Rohwer and Anderson, 1988; Oring and Saylor, 1992; Thompson and Baldassarre, 1992). It is likely that paired birds consistently move together, although the permanence of the movement groups is unknown: it was not possible to identify individual birds during field observation. When $(1 - \gamma_1) = \gamma_2$, G is geometrically distributed. If each bird makes an independent decision to form its own group, with probability γ_2 , then the zero-truncated geometric distribution is the limiting distribution of partitions of the community into groups, as B grows large (Duerr and Dietz, 2000).

According to Eq. (1), group size is unbounded. In reality, group size can not be larger than the number of birds available to move. Thus, if n birds are in the aggregation, no departing group can be larger than n and no arriving group can be larger than $(B - n)$. During field observation, the total number of birds present,

B , was typically much greater than the number in the observed aggregation, n , and also much larger than the average observed group size. Thus, this constraint does not noticeably affect the group size distribution for arriving birds. In contrast, the constraint that departing group size, G_d , be less than the number of birds in the aggregation alters the distribution of G_d when $N(t) = n$ is small. Taking this constraint in account, the distribution of G_d is

$$\begin{aligned} \Pr(G_d = k) &= \Pr(G = k | G \leq n) \\ &= \frac{gk}{1 - \gamma_1(1 - \gamma_2)^{n-1}}, \quad \text{for } k = 1, 2, 3, \dots, n, \end{aligned} \quad (2)$$

where $\Pr(G \leq n) = 1 - \gamma_1(1 - \gamma_2)^{n-1}$.

Appendix A includes derivation of the maximum likelihood rates for the model. The maximum likelihood estimates of r_a and r_d , the per capita arrival and departure rates, can be solved for explicitly, while the estimates of γ_1 and γ_2 must be calculated numerically. The number of birds in the area, B , was estimated from censuses. I do not consider variability in B , as model assessment was insensitive to relatively large changes in this parameter.

2.2. Aggregation observations

To investigate waterfowl social behavior, I conducted a series of aggregation formation observations at the Municipal Wastewater Treatment Facility in Stanwood, Washington, USA. Waterfowl stop at this facility during migration along the Pacific flyway. The site consists of one 35 acre stabilization pond and three 1-acre ponds. I collected data at the Stanwood ponds during 8 days in the fall of 1994 and 11 days in the spring of 1995.

One of the three small, 1-acre ponds served as the observational pond; birds on this pond were defined to be members of an aggregation. The remaining ponds constituted the larger, surrounding area from which birds on the observational pond were drawn. Since few birds entered or left the facility during the course of each individual aggregation observation, I consider the study site as a closed system. Before each observation, I completed a census of the facility by scanning the area with a spotting scope. I then flushed all birds off the observational pond. From a position out of sight,

Table 1
Total birds and number of species in the area by day

Date	Aggregation number	Total birds	Number of species	Max. birds in aggregation	Disturbance
Fall					
Oct 2	1	686	10	104	0
Oct 9	2–3	900	12	11–29	0
Oct 16	4–5	1258	12	5–43	0
Oct 23	6–7	1792	13	79–83	0
Oct 29	8–9	1089	16	48–52	0
Nov 5	10	2858	15	52	0
Nov 11	11	2009	14	40	0
Nov 26	12	1468	13	95	0
Spring					
Feb 18	13–17	873	10	9–50	0
Mar 4	18–21	1094	11	7–27	2
Mar 11	22–24	828	13	26–74	2
Mar 12	25	836	13	22	1
Mar 19	26–28	472	10	27–47	2
Mar 26	29–30	300	10	21–45	1
Apr 2	31–32	546	10	30–60	1
Apr 9	33–34	990	11	34–43	0
Apr 15	35–36	843	11	22–37	2
Apr 22	37–38	1222	13	29–84	2
Apr 29	39	178	9	24	0

Total birds, \bar{B} , are averages of all censuses conducted on each day. Ranges in the maximum number of birds are for multiple aggregation observations conducted on the same day. See text for a description of the disturbance codes.

I kept a continuous time record of movements onto and off of the observational pond with binoculars and a micro-cassette recorder. For a detailed description of both the site and the data collection protocol, see Silverman et al. (2001).

The data consist of 12 aggregation observations from the fall of 1994 and an additional 27 from the spring of 1995 (Table 1). These 39 observations lasted 12–96 min and took place between mid-morning and late afternoon. The more numerous spring observations were divided between days with short, repeated observations (numbers 13–17, 18–21, 22–24, and 26–28) and days with one or two long observations. Table 1 includes the maximum number of birds observed in each aggregation and the number of birds and species at the facility, which varied substantially within and between seasons. Overall, I observed 14 species of ducks representing four tribes (Anatini, Mergini, Aythyini, and Oxyurini) and five other species of aquatic birds (*Podilymbus podiceps*, *Podiceps auritus*, *Phalacrocorax auritus*, *Fulica americana* and *Branta canadensis*). Bald eagles *Haliaeetus leucocephalus* were observed on eight days during the spring. Days when eagles were present are noted

in Table 1. Based on prior analysis of the fit of a simpler model (Silverman et al., 2001), I defined all birds recorded as arriving (or departing) within 2 s of one another to be a movement group.

2.3. Statistical analysis

2.3.1. Model validity

The validity of the assumption that group size has a modified-geometric distribution with parameters γ_1 and γ_2 (Eqs. (1) and (2)) can be assessed by the likelihood ratio test (LRT).

The test statistic for the LRT (Lindgren, 1968) is

$$\Lambda = 2 \ln \left[\frac{\max(L)}{\max(L_o)} \right]. \quad (3)$$

L_o is the likelihood function under the null hypothesis that group size has a modified-geometric distribution and is maximized at the maximum likelihood estimates of γ_1 and γ_2 . L is the likelihood under the “full” model, with no constraint on the group size distribution, $\Pr(G = k) = g_k$, other than

$$\sum_{k=1}^K g_k = 1, \quad (4)$$

where K is the maximum possible group size. Appendix B presents the derivation of the maximum likelihood rates for the full model. If the null hypothesis that group size has a modified-geometric distribution is true, then Λ has a χ^2 -distribution with $(K - 2)$ degrees of freedom (Lindgren, 1968).

Since the estimated maximum likelihood rates for the full model, \hat{g}_k , are zero for all k greater than the largest observed group size, I redefined K for each aggregation to be the maximum group size recorded during that aggregation. There were no groups larger than two birds in three aggregations (13, 16, and 21) and no groups larger than single birds in one (15). The modified-geometric and full models are indistinguishable in these cases and the LRT is not applicable. Groups larger than 10 birds occurred only during aggregation 35 (one group of 16 and one of 20), when two bald eagles flushed the birds off the observational pond. Since these large groups were caused by a disturbance, I set $K = 10$, the next largest group size, for aggregation 35's LRT.

The model also predicts that the intervals between consecutive movement events are exponentially distributed. The validity of this prediction for each aggregation was demonstrated previously (Silverman et al., 2001).

2.3.2. Model simulations

If the model fits the data, the question arises as to whether the model's parameters were constant over all 39 observed aggregations. Constant parameters suggest relatively fixed behavior, while the relationship between variable parameters and other, independent variables can help describe the aggregative behavior of waterfowl. The distinction between constant and variable parameters is determined by considering the variability of the 39 estimates for each parameter. If the underlying value of a parameter is constant, then the variance of its estimates is predictable. Specifically, the asymptotic variance of a maximum likelihood estimator is its information bound evaluated at the parameter value (Appendix A). For non-constant parameters, the estimates will be more variable than the information matrix predicts.

Unfortunately, because the observations differed in length, number of movement events, and number of birds at the facility, B , it is not possible to compare the variability of the 39 estimates to that predicted

from the information matrix (see Appendix A). Thus, I simulated the model with constant parameter values and compared the variability of the resulting parameter estimates to the observed variability. Parameter estimation and all simulations were performed by C programs running on a Dell Latitude LM laptop computer, using a long period random number generator (Press et al., 1992).

The simulation procedure entailed three steps: first, I combined the data from the 39 aggregations and estimated the four parameters using systems (A.3) and (A.5). (See Table 2. For r_a and r_d , the combined estimates average the 39 individual estimates, weighting by the total time of each observation. For γ_1 and γ_2 , the combined estimates are calculated using all observed groups and their corresponding $n^{d,s}$ s); second, using these combined parameter estimates, I simulated the model 39 times using each aggregation's B and total time of observation; third, I re-estimated the model parameters for each of the 39 simulations. This procedure was repeated 100 times, resulting in 100 sets of 39 estimates for the four parameters. A comparison of the 39 estimated standard errors of \hat{r}_a , calculated for each aggregation using the 100 simulations, to the estimated standard errors predicted by the information matrix (Appendix A) revealed that most aggregations had an insufficient number of arrival events to justify using the asymptotic properties of maximum likelihood. This was also true for \hat{r}_d .

Each of the 100 sets of 39 estimates is a realization of the constant parameter model, equivalent to the observed aggregations. Thus, the simulations resulted in 100 estimated coefficients of variation (c.v.), based on a sample size of 39, for \hat{r}_a , \hat{r}_d , $\hat{\gamma}_1$, and $\hat{\gamma}_2$ under the model with constant parameter values. These predicted c.v. can be compared to the four observed c.v. calculated from the data. When an observed c.v. is large, compared to the simulated c.v., the associated parameter estimates are determined to have resulted from a non-constant parameter. Thus, the simulation procedure demonstrates which parameters, and hence which aspects of aggregative behavior, vary more than the stochasticity of the model predicts, if that behavior were constant over all 39 aggregations.

2.3.3. Exploratory analysis of rate estimates

Variable parameters require further consideration. For the parameters that exhibited extra variability, I

Table 2

Maximum likelihood estimates of the per capita arrival and departure rates, r_a and r_d , and the grouping parameters, γ_1 and γ_2 , for the 39 aggregation observations, including the P -values for the likelihood ratio test

Agg. no.	r_a ($\times 10^{-5} \text{s}^{-1}$)	r_d ($\times 10^{-4} \text{s}^{-1}$)	γ_1	γ_2	P	Agg. no.	r_a ($\times 10^{-5} \text{s}^{-1}$)	r_d ($\times 10^{-4} \text{s}^{-1}$)	γ_1	γ_2	P
1	4.11	0.51	0.34	0.37	0.06	22	2.71	1.89	0.54	0.58	0.01
2	0.60	5.06	0.18	0.32	0.28	23	1.73	3.37	0.40	0.90	0.64
3	0.86	0.60	0.38	0.57	0.32	24	2.87	0.57	0.45	0.52	0.02
4	0.11	5.93	0.35	0.71	0.36	25	2.59	4.18	0.22	0.87	0.59
5	0.50	0.48	0.39	0.75	0.09	26	1.57	1.76	0.33	0.92	0.68
6	1.10	1.16	0.23	0.47	0.12	27	2.79	0.64	0.30	0.81	0.24
7	1.20	1.77	0.18	0.56	0.05	28	3.69	0.52	0.56	0.62	0.32
8	1.32	1.69	0.35	0.57	0.22	29	2.52	2.47	0.22	0.87	0.59
9	1.59	3.61	0.16	0.58	0.55	30	3.73	0.00	0.36	0.67	0.11
10	0.56	2.02	0.29	0.73	0.19	31	1.45	0.34	0.33	0.73	0.08
11	0.69	3.40	0.25	0.87	0.28	32	2.78	0.83	0.36	0.69	0.78
12	1.13	0.66	0.24	0.59	0.28	33	1.21	1.58	0.35	0.67	0.07
13	2.82	1.55	0.18	1.00	NA	34	1.03	1.59	0.31	0.87	0.45
14	4.47	1.92	0.19	0.71	0.20	35	2.07	5.07	0.43	0.48	<0.001*
15	1.50	4.87	0.00	NA	NA	36	2.42	8.11	0.28	0.54	0.41
16	1.19	8.72	0.07	1.00	NA	37	1.40	2.98	0.31	0.68	0.01
17	1.35	0.31	0.33	0.55	0.61	38	0.85	1.24	0.38	0.92	0.67
18	0.73	15.72	0.24	0.82	0.51	39	3.18	2.16	0.31	0.63	0.07
19	1.55	5.67	0.23	0.84	0.39	Mean	1.80	2.69	0.30	0.71	
20	1.23	0.00	0.46	0.86	0.18	S.D.	1.08	3.06	0.11	0.18	
21	1.03	0.00	0.30	1.00	NA	Combined	1.24	1.83	0.30	0.62	

The superscript (*) indicates statistical significance when an individual test's α -level is 0.0014, ensuring an overall α -level of 0.05. The mean and standard deviation of the 39 estimates for each of the four parameters are included, as are the four parameter estimates calculated from the data for all 39 observations combined.

compared the estimates for aggregations classified by day of observation, season, and level of disturbance. I used non-parametric statistical procedures (Kruskal–Wallis and Mann–Whitney U tests, see (Zar, 1996)), since the simulations demonstrated that the maximum likelihood estimates were not close to normal. Level of disturbance was defined by the presence of bald eagles in and around the facility. Days were classified as (0) no eagle present, (1) an eagle present before or after the observations, and (2) an eagle flying over during one or more of the observations. One instance of gunfire, which also disturbed the birds, was classified as a (2) disturbance.

3. Results

The maximum likelihood estimates for the 39 aggregation observations are reported in Table 2. Aggregation 15, with $\hat{\gamma}_1 = 0$, had only solitary arrivals and

departures. Aggregations 13, 16, and 21, with $\hat{\gamma}_2 = 1.0$, had no groups of more than two birds. Aggregations 3, 10, 24, 30, 32, 33, and 37 had group distributions close to geometric, since $\hat{\gamma}_1 + \hat{\gamma}_2 \approx 1$. Table 2 also reports the mean and standard deviation of the 39 estimates, and the parameter estimates calculated using the data from all 39 aggregations combined.

3.1. Model fit

The likelihood ratio test rejects the fit of the modified-geometric distribution to the observed group size distributions only for aggregation 35, when eagles disturbed the aggregation (Table 2). Two other aggregations (22 and 37) had small P -values. An eagle also flew over during observation of aggregation 22, but cannot explain the marginal fit of the modified-geometric to aggregation 37. Barring disturbance, the group size data seem to be well described by the modified-geometric distribution.

To characterize the group size distribution simultaneously for all 39 aggregations, I randomly sampled one group from each aggregation and estimated the observed group size distribution based on this 39 group sample. The procedure was repeated 250 times, resulting in 250 estimated group size distributions. Fig. 1 plots the average proportion of times each group size was observed, along with the 5th and 95th percentiles, from the 250 estimated distributions. The modified-geometric probability distribution, based on the combined maximum likelihood estimates, $\hat{\gamma}_1 = 0.30$ and $\hat{\gamma}_2 = 0.62$ (Table 2), is included in Fig. 1. The figure suggests a close fit between the observed distribution of group sizes and the distribution predicted by the modified-geometric distribution when the data from all 39 aggregations are combined.

Silverman et al. (2001) demonstrated that, if all birds arriving (or departing) within 2 s of one another constituted a movement group, then the exponential distribution reasonably described the time intervals between successive movement events.

3.2. Parameter variability

Since the model is a good descriptor of the field observations, it is reasonable to explore if all 39 aggregations could have resulted from one set of constant, underlying parameter values. Model simulations address this question and reveal that the movement rates, but not group sizes, differed among aggregations.

The range of c.v. for the 100 simulated sets of \hat{r}_a was 0.16–0.32. This is within the range that predicted by the information matrix (see Appendix A): 0.10, based on the maximum number of arrivals, $A = 105$, for aggregation 7, and 0.41, based on the minimum $A = 6$, for aggregation 4. The observed c.v. for \hat{r}_a was 0.63, well above both these ranges. Similarly, the range of simulated c.v. for \hat{r}_d was 0.37–0.91; the range predicted by the information matrix and based on the minimum and maximum D (greater than zero) was 0.14–1.0. The \hat{r}_d 's observed c.v. was 1.16. These results suggest that the 39 aggregations had different per capita movement rates.

The observed c.v. for $\hat{\gamma}_1$ and $\hat{\gamma}_2$, 0.38 and 0.25, fell well within the simulated ranges of [0.21, 0.48] and [0.17, 0.40], respectively. Seventeen of the 100 simulated c.v. for $\hat{\gamma}_1$ exceeded the observed c.v. and 49 of the 100 simulated c.v. for $\hat{\gamma}_2$ exceeded the observed.

By this measure, there is no evidence that the grouping parameters vary across the 39 aggregations.

3.3. Factors affecting movement rates

The estimated group movement rates, \hat{r}_a and \hat{r}_d , are more variable than the constant parameter model predicts. Understanding when these parameters change will contribute to understanding the aggregative behavior of waterfowl. A brief exploratory analysis suggests several avenues for further investigation.

Movement rates differed from week to week: specifically, there were more differences among the average arrival rates over the 19 days of observation than among the arrival rates observed on the same day (Kruskal–Wallis, $P = 0.03$). This result is not surprising, since multiple aggregations on the same day likely included some of the same birds. Despite the significant day effect for r_a , the parameters' estimates did not exhibit noticeable patterns when plotted by time in the season for either migratory period. Departure rates, which were extremely variable (c.v. = 1.16), did not show a significant day effect ($P = 0.86$).

Because of the significant day effect for r_a , I used the average daily arrival and departure rates ($n = 19$) in all subsequent analyses. Arrival rate onto the observational pond, averaged by day of observation, was significantly greater in spring than in fall (Mann–Whitney test, $P = 0.04$, $n_{\text{fall}} = 8$, $n_{\text{spring}} = 11$, fall mean = $1.27 \times 10^{-5} \text{ s}^{-1}$, spring mean = $2.18 \times 10^{-5} \text{ s}^{-1}$, difference in means in units of standard deviation = 0.87). There was no significant difference between fall and spring departure rates (Mann–Whitney test, $P = 0.60$, $n_{\text{fall}} = 8$, $n_{\text{spring}} = 11$, fall mean = $2.09 \times 10^{-4} \text{ s}^{-1}$, spring mean = $2.74 \times 10^{-4} \text{ s}^{-1}$, standardized difference in means = 0.40).

Bald eagles were present only in the spring, but their presence does not appear to explain the observed seasonal differences in movement rates. Considering the 11 spring days, of which three were classified as disturbance level 0, three were level 1, and five were level 2 (Table 1), there were no significant differences in movement rates attributable to disturbance (Kruskal–Wallis, $P = 0.68$ for the arrival rate test and $P = 0.58$ for the departure rate test). The mean arrival rates by disturbance class were $2.19 \times 10^{-5} \text{ s}^{-1}$ for no

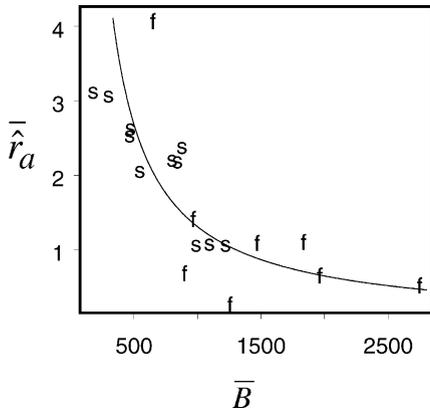


Fig. 2. Average daily arrival rates estimates, $\hat{r}_a (\times 10^{-5} s^{-1})$, vs. the average number of birds, \bar{B} , counted in the censuses. *S* = spring observation. *F* = fall observation. The curve represents the right-hand side of Eq. (A.3a) plotted as a function of B for data from all the aggregations combined.

disturbance, $2.61 \times 10^{-5} s^{-1}$ for level 1, and $1.93 \times 10^{-5} s^{-1}$ for level 2 (standardized differences between consecutive means = 0.35 and 0.56). The mean departure rates were $2.41 \times 10^{-4} s^{-1}$ for no disturbance, $2.00 \times 10^{-4} s^{-1}$ for level 1, and $3.39 \times 10^{-4} s^{-1}$ for level 2 (standardized differences between consecutive means = 0.22 and 0.51).

Besides the effect of season, the clearest factor affecting arrival rate into the aggregations was the number of birds at the facility, B . Fig. 2 illustrates this density effect: \hat{r}_a declines with increasing waterfowl density. If per capita arrival rates were not density-dependent, increasing B should correspond to an increase in the number of arrivals, A , so that the numerator of Eq. (A.3a) increases with the denominator. Fig. 2 includes the expected relationship between r_a and B , if the number of arrivals was constant. This curve is the right hand side of Eq. (A.3a), plotted as a function of B with A equal to the total number of arrivals observed in all aggregations and using all observed Δt_j 's and n_j 's.

4. Discussion

I observed aggregation formation over a variety of conditions during two migratory seasons. Community composition, measured as relative species abundance, changed throughout the two seasons and the number

of birds present varied from hundreds to thousands (Table 1, see also Silverman et al., 2001). Despite these fluctuations, there is no evidence that the proposed model fails to describe the observed aggregations. Although failure to reject does not mean that the model correctly describes the phenomenon of interest, both the close fit of the model and the simulation results highlight several characteristics of waterfowl aggregation at the Stanwood site.

First, the observed multi-species aggregation process does not deviate significantly from a neutral model (Caswell, 1976) that treats all species identically. Second, the observed movement groups are described by a simple, two parameter distribution that does not depend on aggregation size. In some cases the even simpler geometric distribution may be sufficient describe the group sizes (i.e., $\gamma_1 + \gamma_2 = 1$); the reasonableness of the geometric distribution does not appear to be related to increases in B , however, as would be expected with Duerr and Dietz's (2000) model. In either case, the parameters of the modified-geometric distribution of group size did not vary substantially among the 39 aggregations, the 19 days of observation, nor the two migratory seasons. Third, exponentially distributed interevent times suggest that group movements are independent of one another and the aggregation process is homogeneous in time, with little change in behavior as bird numbers increase on the observational pond. In this system, birds outside the observational pond were typically clustered together and transit time was minimal; in situations where birds join an aggregation from widely separated sources, the exponential distribution could fail to describe the arrival intervals. Finally, these results hold for the initial stages of aggregation formation, when the process is far from equilibrium. Based on these findings and despite shifting community composition, the observed waterfowl behavior was surprisingly uncomplicated. These results are similar to those of Evans (1982) and Evans and Welham (1985), who describe departures of gulls from breeding colonies as the combination of random departure times and social attraction.

When bald eagles flew directly over the aggregations, they provoked pandemonium, with many groups taking flight in close succession (the single instance of gunfire had the same effect). This is to be expected, since eagles are known to feed on waterfowl (Todd

et al., 1982; Watson et al., 1991, personal observation). In several cases, such disturbance was sufficient to terminate observation of the aggregations; the model's requirement of independent, exponentially distributed interevent times most certainly was violated during these incidents. Similarly, the likelihood ratio test rejected a modified-geometric group size distribution when eagles were active. Since the model's predictions failed only when bald eagles flew over the ponds, I argue that failure to reject the model in the remaining cases is not due solely to low power. The few model failures, attributable to immediate disturbance, strengthen confidence in the fit of the model, since the statistical tests detected when the process broke down.

Despite a clear disturbance effect, eagles appear to influence waterfowl behavior only temporarily: parameter estimates for days of disturbance are not distinguishable from estimates for disturbance free days. The estimated means and the differences between them show no clear pattern of predator effect. Of course, a larger sample of days or observation of other aspects of aggregative behavior might well reveal behavioral effects undetected here.

In contrast to group sizes, movement rates into and out of the aggregations were more variable than the model predicts, if all 39 aggregations were generated by the same, constant parameter values. Further analysis revealed that birds were more likely to fly into the observational pond during the spring. Moreover, although departure rates did not differ significantly between the seasons, the average spring departure rate was higher than the average fall departure rate. These results suggest a generally higher activity level among birds migrating north to breed than among southward migrating birds.

There were no within season patterns in the estimated movement rates. Besides differences between the spring and fall, the most important variable affecting movement was the total density of birds at the facility. Arrival rates into the aggregations were high at low density and low at high density. It appears that individual birds are attracted to aggregations on the more sheltered observational pond when community abundance is low. At high community abundance, the density of birds on the observational pond may not differ enough from the surrounding area to make it a specially attractive location. This pattern was also observed in the estimates for a simpler model (Silverman

and Kot, 2000), which did not incorporate group movements, although the group-movement model provides improved movement rate estimates, due to its better fit.

The dynamical model proposed here describes the general features of mixed-species waterfowl aggregation and is a useful method for investigating complex animal behavior. Comparison of the expected variability in the parameter estimates, assuming constant parameters for all the observations, to the observed variability revealed both behaviors that changed over the time-scale of the observations and behaviors that did not. Given the distinct end points of fall and spring migration, the lack of differences in group distributions is notable. But, more extensive data collection is necessary to determine the generalizability of this result. This model serves as a framework for exploring interspecific differences in aggregation behavior, through consideration of the movement rates and group sizes of distinct subsets of species (Silverman, manuscript). Similar models might usefully be applied to the social dynamics of other species.

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Appendix A

The likelihood function for the model, derived using standard methods (Guttorp, 1995), is

$$L = \prod_{j=1}^A r_a (B - n_j^a) g_{k_j} \prod_{j=1}^D r_d n_j^d \frac{g_{k_j}}{\sum_{k=1}^{n_j^d} g_k} \times \prod_{j=0}^{A+D} e^{-[r_a(B-n_j) + r_d n_j] \Delta t_j}, \tag{A.1}$$

where n_j is the number of birds in the aggregation at time t_j and $\Delta t_j = (t_{j+1} - t_j)$ the time between the $(j + 1)$ th and j th events. A is the total number of arrivals, D is the total number of departures. The n_j^a 's are the n_j 's followed by an arrival and the n_j^d 's are the n_j 's followed by a departure. The k_j 's are the sizes of groups entering or leaving the experimental pond from the corresponding n_j^a or n_j^d .

The natural logarithm of the likelihood function, Eq. (A.1), is

$$l = A \ln(r_a) + D \ln(r_d) + \sum_{j=1}^A \ln(B - n_j^a) + \sum_{j=1}^D \ln(n_j^d) + \sum_{j=1}^{A+D} \ln(g_{k_j}) - \sum_{j=1}^D \ln \left(\sum_{k=1}^{n_j^d} g_k \right) - \sum_{j=0}^{A+D} [r_a(B - n_j) + r_d n_j] \Delta t_j. \tag{A.2}$$

This equation can be used to find the maximum likelihood estimators of the arrival and departure rates,

$$\hat{r}_a = \frac{A}{\sum_{j=0}^{A+D} (B - n_j) \Delta t_j}, \tag{A.3a}$$

$$\hat{r}_d = \frac{D}{\sum_{j=0}^{A+D} n_j \Delta t_j}. \tag{A.3b}$$

The grouping parameters, γ_1 and γ_2 , enter the log-likelihood function in the fifth and sixth terms of Eq. (A.2),

$$\sum_{j=1}^{A+D} \ln g_{k_j} - \sum_{j=1}^D \ln \left(\sum_{k=1}^{n_j^d} g_k \right) = \sum_{\text{all } k=1} \ln(1 - \gamma_1) + \sum_{\text{all } k \geq 2} \ln[\gamma_1 \gamma_2 (1 - \gamma_2)^{k-2}] - \sum_{j=1}^D \ln[1 - \gamma_1 (1 - \gamma_2)^{n_j^d - 1}] \tag{A.4a}$$

$$\sum_{j=1}^{A+D} \ln g_{k_j} - \sum_{j=1}^D \ln \left(\sum_{k=1}^{n_j^d} g_k \right) = (A_1 + D_1) \ln(1 - \gamma_1) + (A_2 + D_2) [\ln \gamma_1 + \ln \gamma_2] + \ln(1 - \gamma_2) \sum_{\text{all } k \geq 2} (k - 2) - \sum_{j=1}^D \ln[1 - \gamma_1 (1 - \gamma_2)^{n_j^d - 1}], \tag{A.4b}$$

where A_1 is the number of single arrivals, A_2 is the number of arrivals of two or more birds, D_1 is the number of single departures, and D_2 is the number of departures of two or more birds.

Thus, the maximum likelihood estimates of γ_1 and γ_2 are found by simultaneously solving

$$\frac{\gamma_1(A + D) - (A_2 + D_2)}{\gamma_1(1 - \gamma_1)} = \sum_{j=1}^D \frac{(1 - \gamma_2)^{n_j^d - 1}}{[1 - \gamma_1(1 - \gamma_2)^{n_j^d - 1}]}, \tag{A.5a}$$

$$\frac{A_2 + D_2}{\gamma_2} - \frac{\sum_{j=1}^{A_2+D_2} (k_j^{(2)} - 2)}{(1 - \gamma_2)} = \sum_{j=1}^D \frac{\gamma_1(n_j^d - 1)(1 - \gamma_2)^{n_j^d - 2}}{[1 - \gamma_1(1 - \gamma_2)^{n_j^d - 1}]}, \tag{A.5b}$$

with both parameters constrained to take values between zero and one. The $k_j^{(2)}$'s are the sizes of all groups of two or more birds. Since system (A.5) cannot be solved explicitly for γ_1 and γ_2 , I estimated these two parameters numerically. I conducted an exhaustive search of (γ_1, γ_2) parameter space, evaluating Eq. (A.4b) for 1000×1000 possible pairs (γ_1, γ_2) ; $\hat{\gamma}_1$ and $\hat{\gamma}_2$ were the pair which maximized the log-likelihood, Eq. (A.4b).

The asymptotic variance-covariance matrix of the maximum likelihood estimators, the Fisher information matrix, is calculated as the inverse of the negative 4×4 Hessian matrix of l , the (i, j) th element of which is

$$-\frac{\partial^2 l(\vec{\theta})}{\partial \theta_i \partial \theta_j}, \tag{A.6}$$

where $\vec{\theta} = (r_a, r_d, \gamma_1, \gamma_2)$ (Arnold, 1990).

Thus, the asymptotic variances of \hat{r}_a and \hat{r}_d are

$$\left(-\frac{\partial^2 l}{\partial r_a^2}\right)^{-1} = \frac{r_a^2}{A}, \tag{A.7a}$$

$$\left(-\frac{\partial^2 l}{\partial r_d^2}\right)^{-1} = \frac{r_d^2}{D}. \tag{A.7b}$$

So that the coefficients of variation of \hat{r}_a and \hat{r}_d are $1/\sqrt{A}$ and $1/\sqrt{D}$, respectively.

The asymptotic variances of $\hat{\gamma}_1$ and $\hat{\gamma}_2$ are found by moving all the terms in Eqs. (A.5a) and (A.5b) and to the right hand side, differentiating with respect to γ_1 and γ_2 , respectively, and taking the inverse of the resulting expressions.

Appendix B

Under the full model, the only constraint on the distribution of group size, G , is that the g_k 's—where $\Pr(G = k) = g_k$ for $k = 1, 2, 3, \dots, K$ and K is the maximum possible group size—must sum to one. For this model,

$$\sum_{j=1}^{A+D} \ln g_{k_j} - \sum_{j=1}^D \ln \left(\sum_{k=1}^{n_j^d} g_k \right) = \sum_{k=1}^K (X_k \ln g_k) - \sum_{k=1}^{K-1} \left[Y_k \ln \left(\sum_{l=1}^k g_l \right) \right], \tag{B.1}$$

where

$$X_k = \text{Number of groups of size } k, \tag{B.2a}$$

$$Y_k = \text{Number of } n_j^d = k. \tag{B.2b}$$

Standard methods and a lot of algebra lead to the following maximum likelihood estimators,

$$\hat{g}_1 = \frac{Z_1 \cdot Z_2 \cdots Z_{K-1}}{(Z_1 + X_2) \cdot (Z_2 + X_3) \cdots (Z_{K-1} + X_K)}, \tag{B.3a}$$

$$\hat{g}_2 = \frac{X_2 \cdot Z_2 \cdot Z_3 \cdots Z_{K-1}}{(Z_1 + X_2) \cdot (Z_2 + X_3) \cdots (Z_{K-1} + X_K)}, \tag{B.3b}$$

$$\hat{g}_3 = \frac{X_3 \cdot Z_3 \cdot Z_4 \cdots Z_{K-1}}{(Z_2 + X_3) \cdot (Z_3 + X_4) \cdots (Z_{K-1} + X_K)}, \tag{B.3c}$$

$$\vdots \qquad \qquad \qquad \vdots$$

$$\hat{g}_{K-1} = \frac{X_{K-1} \cdot Z_{K-1}}{(Z_{K-2} + X_{K-1}) \cdot (Z_{K-1} + X_K)}, \tag{B.3d}$$

$$\hat{g}_K = \frac{X_K}{Z_{K-1} + X_K}, \tag{B.3e}$$

where

$$Z_k = \sum_{j=1}^k (X_j - Y_j). \tag{B.4}$$

The likelihood function (Eq. (A.1)), evaluated using the \hat{g}_k 's from system (B.3), is the numerator of the likelihood ratio test described in the text.

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