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Claire S. Teitelbaum
Akima Systems Engineering

Michael L. Casazza
United States Geological Survey Western Region

Fiona McDuie
San Jose State University, fiona.mcduie@sjsu.edu

Susan E.W. De La Cruz
U.S. Geological Survey Western Ecological Research Center

Cory T. Overton
United States Geological Survey Western Region

See next page for additional authors

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ARTICLE
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Waterfowl recently infected with low pathogenic avian influenza exhibit reduced local movement and delayed migration

Claire S. Teitelbaum[1,2] | **Michael L. Casazza**[3] | **Fiona McDuie**[3,4] | **Susan E. W. De La Cruz**[5] | **Cory T. Overton**[3] | **Laurie A. Hall**[5] | **Elliott L. Matchett**[3] | **Joshua T. Ackerman**[3] | **Jeffery D. Sullivan**[6] | **Andrew M. Ramey**[7] | **Diann J. Prosser**[6]

[1]Akima Systems Engineering, Herndon, Virginia, USA

[2]Contractor to U.S. Geological Survey Eastern Ecological Science Center, Laurel, Maryland, USA

[3]U.S. Geological Survey Western Ecological Research Center, Dixon Field Station, Dixon, California, USA

[4]San Jose State University Research Foundation, Moss Landing Marine Laboratories, Moss Landing, California, USA

[5]U.S. Geological Survey Western Ecological Research Center, San Francisco Bay Estuary Field Station, Moffett Field, California, USA

[6]U.S. Geological Survey Eastern Ecological Science Center, Laurel, Maryland, USA

[7]U.S. Geological Survey Alaska Science Center, Anchorage, Alaska, USA

Correspondence
Diann J. Prosser
Email: dprosser@usgs.gov

Funding information
California Department of Water Resources; Ducks Unlimited; U.S. Geological Survey Ecosystems Mission Area

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Abstract

Understanding relationships between infection and wildlife movement patterns is important for predicting pathogen spread, especially for multispecies pathogens and those that can spread to humans and domestic animals, such as avian influenza viruses (AIVs). Although infection with low pathogenic AIVs is generally considered asymptomatic in wild birds, prior work has shown that influenza-infected birds occasionally delay migration and/or reduce local movements relative to their uninfected counterparts. However, most observational research to date has focused on a few species in northern Europe; given that influenza viruses are widespread globally and outbreaks of highly pathogenic strains are increasingly common, it is important to explore influenza–movement relationships across more species and regions. Here, we used telemetry data to investigate relationships between influenza infection and movement behavior in 165 individuals from four species of North American waterfowl that overwinter in California, USA. We studied both large-scale migratory and local overwintering movements and found that relationships between influenza infection and movement patterns varied among species. Northern pintails (*Anas acuta*) with antibodies to avian influenza, indicating prior infection, made migratory stopovers that averaged 12 days longer than those with no influenza antibodies. In contrast, greater white-fronted geese (*Anser albifrons*) with antibodies to avian influenza made migratory stopovers that averaged 15 days shorter than those with no antibodies. Canvasbacks (*Aythya valisineria*) that were actively infected with influenza upon capture in the winter delayed spring migration by an average of 28 days relative to birds that were uninfected at the time of capture. At the local scale, northern pintails and canvasbacks that were actively infected with influenza used areas that were 7.6 and 4.9 times smaller

than those of uninfected ducks, respectively, during the period of presumed active influenza infection. We found no evidence for an influence of active influenza infection on local movements of mallards (*Anas platyrhynchos*). These results suggest that avian influenza can influence waterfowl movements and illustrate that the relationships between avian influenza infection and wild bird movements are context- and species-dependent. More generally, understanding and predicting the spread of multihost pathogens requires studying multiple taxa across space and time.

KEYWORDS
animal movement, avian influenza, infectious disease, migration, space use, waterfowl

INTRODUCTION

Knowledge of animal movement patterns is crucial for understanding pathogen transmission because movements govern animals' interactions with one another and with contaminated habitats (Boulinier et al., 2016; Daversa et al., 2017; Shaw et al., 2018). Seasonal migration is often particularly important for host–pathogen interactions because migrants can transport pathogens over long distances (Fritzsche McKay & Hoye, 2016). Moreover, infections can affect animal migration patterns; for example, some infections cause more severe disease during host migration (Buehler et al., 2010), occasionally to the point of reducing a host's probability of migrating or survival during migration (Bartel et al., 2011; Emmenegger et al., 2018). Migration can also reduce infection prevalence in migratory hosts by allowing escape from contaminated habitats (Altizer et al., 2011; Shaw & Binning, 2016). Therefore, the strength and direction of the relationships between infection and animal movement depend on the interactions between host biology, pathogen biology, and the environmental context (Risely et al., 2018).

Bird migration plays a prominent role in the transmission and spread of avian influenza viruses (AIVs), which are important pathogens that affect wildlife, livestock, and occasionally human health. Wild waterfowl, including ducks, geese, and swans, are natural reservoirs of influenza viruses (Webster et al., 1992), and a majority of these species are migratory (Green, 1996). Waterfowl maintain low pathogenic avian influenza viruses (LPAIVs) within populations, including subtypes that have the potential to develop high pathogenicity in poultry, where they cause substantial mortality. Migrants disperse LPAIVs across space (Humphreys et al., 2020; van Dijk et al., 2014) and could play an important role in the maintenance and dispersal of Goose/Guangdong lineage clade 2.3.4.4 highly pathogenic avian influenza virus (HPAIV). HPAIV, which is an emerging disease threat to both poultry and wild birds, can be transmitted within and between wild bird and poultry populations through multiple routes, including a fecal-oral route during foraging, environmentally persistent virions in water, and potentially through direct contact or contaminated objects (Ramey, Hill, et al., 2022). Migration of wild birds is the leading hypothesis for the origin of the ongoing novel outbreaks of HPAIV in North America (Bevins et al., 2022; Caliendo et al., 2022).

Although LPAIV infection usually causes few or no clinical signs in wild birds (Kuiken, 2013), observational studies suggest that LPAIV-infected birds sometimes migrate later or move less than uninfected birds (Table 1), indicating that LPAIV infection could have sublethal effects on bird health. However, this evidence is mixed: effects are only sometimes detected and are often small (Table 1). As is true for the effects of any sickness behavior (e.g., lethargy, anorexia) on infectious disease transmission (Hart, 1988), the effects of influenza infection on wild bird movement could influence the spread of endemic LPAIV and, ultimately, HPAIV. For example, infection-induced delays in migration could reduce transmission by limiting contact between infected and uninfected hosts at stopover sites, where birds stop to rest and feed during migration (Galsworthy et al., 2011). Changes in local (i.e., nonmigratory) movements in infected birds could also alter LPAIV dynamics since LPAIV transmission occurs year-round, including during winter and migratory stopover (Hill et al., 2012). For instance, reduced movements by infected birds could decrease the number of contacts per infected bird, thus limiting direct transmission, or could increase environmental transmission rates if longer residence times result in higher concentrations of virus in the environment (Park, 2012). Observed changes in movement patterns with LPAIV infection range from no effect (Bengtsson et al., 2016) to a 1-month delay in migration (van Gils et al., 2007), indicating that the effects of LPAIV on waterfowl movement and migration are species- and

TABLE 1 Results from prior studies examining the relationship between avian influenza virus (AIV) infection and movement behavior in wild waterfowl (Anseriformes) for previous observational studies.

Species	Movement metric	Result	Season	Location	LPAIV prev.[a]	*N*[b]	Reference
Bewick's swan (*Cygnus columbianus bewickii*)	Spring migration departure date; stopover distance	Later departure and closer first stopover in infected birds.	Winter and spring migration	Netherlands	0.17	12	van Gils et al. (2007)
Mallard (*Anas platyrhynchos*)	Stopover duration; migration speed and duration	Longer stopover with higher viral loads among infected birds. Varied by month. No effect of infection on migration speed or distance.	Autumn migration	Sweden	0.07	129	Latorre-Margalef et al. (2009)
Greater white-fronted goose (*Anser albifrons*)	Mean maximum resighting distance 1–12 days post sampling	No effect of infection.	Winter	Netherlands	0.10	503	Kleijn et al. (2010)
Mallard	No. short-distance movements; daily space use; daily time away from roost	Less movement in poor weather in infected birds. Varied by month. No difference in movement between infected and uninfected periods in individuals that were resampled for AIV.	Autumn migration	Netherlands	0.14	71	van Dijk et al. (2015)
Bewick's swan	Timing and distance of departure from capture site	Later dispersal and shorter dispersal distance in infected birds. Depended on metric used.	Winter	Netherlands	0.23	82	Hoye et al. (2016)
Mallard	Movement distance, speed, and dispersion; first passage time; space use	No effect of infection.	Autumn migration	Sweden	0.50[c]	40	Bengtsson et al. (2016)

Abbreviation: LPAIV, low pathogenic avian influenza virus.

[a]All studies measured active infection with low pathogenic AIVs and prevalence (prev.) is the proportion of sampled birds that tested positive for LPAIV infection.

[b]Total sample sizes (*N*) include the number of infected and uninfected birds considered in each study.

[c]Birds were selected for tracking based on infection status, so infection prevalence does not represent that of a population sample.

context-dependent. However, past studies have focused primarily on two species (mallards *Anas platyrhynchos* and Bewick's swans *Cygnus bewickii*) and, to our knowledge, have all been conducted in northern Europe (Table 1). This taxonomic and geographic focus is notable given that LPAIV prevalence differs across wild bird species (Hill et al., 2010; van Dijk et al., 2018) and that each continent has distinct dominant strains of LPAIV (Widjaja et al., 2004), which differ in their transmissibility and infectious periods (Niqueux et al., 2014).

Here, we combine telemetry data with field sampling for avian influenza to explore relationships between influenza infection and movement behavior in four North American waterfowl species captured in California, USA: mallards, northern pintails (*Anas acuta*), canvasbacks (*Aythya valisineria*), and Pacific greater white-fronted

geese (*Anser albifrons sponsa*). We study the relationship between prior influenza infection and the timing of the subsequent spring migration, then quantify space use and movement distances to explore relationships between active influenza infection and local movement patterns.

METHODS

Study system and field data collection

Ducks and geese were captured, fitted with transmitters, and sampled for active influenza infection and influenza antibodies at multiple sites in California's Central Valley and San Francisco Bay Estuary from 2016 to 2019. In the region, wintering mallards can be either migratory or breed locally, with approximately 60% breeding within California (De Sobrino et al., 2017) and many migrants making relatively short-distance migrations (300–600 km; De Sobrino et al., 2017; Kohl et al., 2022). Northern pintails, canvasbacks, and greater white-fronted geese that winter in the Central Valley and San Francisco Bay Estuary are primarily long-distance migrants, many of which breed in Alaska and the mid-continent Prairie Pothole Region of southern Canada and northern United States (Cook et al., 2021; Ely & Takekawa, 1996; Miller et al., 2005). The Central Valley supports ~6–7 million wintering waterfowl, which inhabit protected wetlands as well as the surrounding agricultural lands (Ackerman et al., 2014; Gilmer et al., 1982). The San Francisco Bay Estuary supports more than 700,000 overwintering waterfowl (Accurso, 1992), of which canvasbacks are among the most numerous diving ducks during winter (Accurso, 1992; Collins & Trost, 2009).

Capture timing, locations, and techniques varied by species and included funnel traps, rocket/cannon nets, swim-in corrals, and handheld dip nets. For more details on capture and marking, see Appendix S1: Supplementary Methods and Figure S1, McDuie, Casazza, Overton, et al. (2019), and McDuie et al. (2022). Pintails were captured in September, October, and February 2016–2019 in and near Suisun Marsh (San Francisco Bay Estuary; 38.138, −121.978), Colusa National Wildlife Refuge (NWR; 39.145, −122.044), and the Upper Butte Basin Wildlife Area (WA) in the Central Valley (39.467, −121.877). Mallards were captured during April–August from 2016 to 2019 at Suisun Marsh and Sacramento NWR (39.425, −122.164). White-fronted geese were captured in September and October 2018 at Sacramento NWR, Colusa NWR, and Gray Lodge WA (39.318, −121.820). Canvasbacks were captured using baited, swim-in corral traps during November–March from 2016 to 2019 at San Pablo Bay (38.123, −122.289) and San Francisco Bay NWR (37.531, −122.071). Birds were fitted with GPS–GSM transmitters or Platform Transmitter Terminals (PTTs), which were attached using elastic harnesses (mallards, northern pintails, and geese) or implanted (canvasbacks).

GPS–GSM transmitters were programmed to provide locations (hereafter "fixes") at varying frequencies depending on battery levels and transmitter types. For dabbling ducks and geese, transmitters provided fixes at 15-min to 6-h intervals and 5-min to 6-h intervals, respectively, depending on battery level. For canvasbacks, PTTs were programmed to provide a fix every 40–216 h, and GPS–GSM units were programmed to provide fixes at 3-h intervals. To ensure data quality and remove potentially invalid fixes, we calculated the apparent speed at each fix as the distance moved between consecutive fixes divided by time interval between fixes and removed any points with an incoming apparent speed >80 km/h, which is the approximate maximum flight speed of many duck and goose species (Cooke, 1933; McDuie, Casazza, Keiter, et al., 2019). Movement data used in this study are published on the U.S. Geological Survey's ScienceBase (Teitelbaum, Casazza, et al., 2022).

Influenza virus and antibody detection

Cloacal swabs and oropharyngeal swabs were taken from captured and tagged birds to test for the presence of avian influenza RNA (i.e., active infection), and blood samples were taken to test for detectable antibodies to avian influenza (i.e., prior infection). Swabs and blood samples were taken from the same bird if possible, but not all birds had paired results for active infection and antibodies because of limitations on sampling and sample processing (Appendix S1: Figure S2). Cloacal and oropharyngeal swabs were collected from the same bird using sterile polyester-tipped applicators, placed together (by bird) in vials containing cold virus transport medium (Ip et al., 2012), and transported on ice to the laboratory, where they were stored at −80°C until processing. Blood samples were collected from jugular veins and stored on ice until processing.

To test cloacal and oropharyngeal swabs for the presence of influenza RNA, we used real-time reverse transcriptase-polymerase chain reaction (rRT-PCR) targeting the matrix gene (Spackman et al., 2002). Viral RNA was extracted from swab samples using MagMAX-96 AI/ND Viral RNA Isolation Kits (Ambion/Applied Biosystems, Foster City, CA) on a KingFisher Magnetic Particle Processor (Thermo Scientific, Waltham, MA). The rRT-PCR was set up using the AgPath-ID One-Step RT-PCR mix (Applied Biosystems, Foster City, CA) and an ABI 7500 real-time PCR system (Applied Biosystems, Foster City, CA). We considered a sample to be rRT-PCR-positive, that

is, to indicate active influenza infection, if the cycle threshold (Ct) value was ≤45 (Ramey et al., 2017). All rRT-PCR-positive samples were further screened for highly pathogenic clade 2.3.4.4 viruses (Ramey et al., 2017); all samples tested negative in this assay and thus were inferred to represent infection with LPAIV.

In the laboratory, blood samples were centrifuged for 10–15 min at >2500 rpm and decanted to extract sera. Sera were extracted and stored at −80°C within 12 h of collection. Sera samples were tested for the presence of influenza A antibodies using commercially available blocking enzyme-linked immunoassay (bELISA; AI MultiS-Screen Avian Influenza Virus Antibody Test Kit; IDEXX Laboratories, Westbrook, ME) and following the manufacturer's instructions. We considered samples with a signal-to-noise (S:N) ratio <0.5 to be positive for the presence of influenza antibodies, indicating prior infection (Brown et al., 2009; van Dijk et al., 2020); detectable antibodies to influenza generally last 6 months to 1.5 years (Fereidouni et al., 2010; Hoye et al., 2011; Shriner et al., 2021), but usually peak within 3 weeks of infection (Fereidouni et al., 2010; Shriner et al., 2021). All antibody detections were assumed to represent prior infection with LPAIVs, since HPAIVs were not known to be present in North America in the year preceding sampling; however, it was not possible to confirm the subtype or viral diversity that produced these prior infections. Some individuals that were actively infected (i.e., rRT-PCR-positive) also had antibodies (i.e., bELISA-positive), which could have resulted either from seroconversion from the current infection or from a prior infection. Infection data are published on the U.S. Geological Survey's ScienceBase (Teitelbaum, Casazza, et al., 2022).

Migration timing

To analyze the timing of migration, we first used telemetry data to classify an individual's movement track into wintering, migration, and breeding phases for the three fully migratory species (canvasbacks, northern pintails, and greater white-fronted geese). To do so, we used net displacement to characterize an individual's location over time, which has the advantage of combining latitude and longitude into a single variable that can be used to characterize migratory behavior (Bunnefeld et al., 2011). We calculated the Euclidean distance (in meters) from a reference point to each location in an individual's movement track (i.e., GPS or PTT fix), producing a time series of location (net displacement) over time. We used the date closest to 31 December of the first year an individual was tracked as the arbitrary reference point of the track, so that at least one overwintering point would have a net displacement of zero.

Next, we used a thresholding approach (Dzialak et al., 2015; Edelhoff et al., 2016) to identify long-distance movements, which we used to separate the track into discrete periods. A long-distance movement was defined as a single calendar day where an individual's average net displacement changed by at least 100 km; we used this 100-km threshold because initial exploratory analyses indicated that it was the distance that best detected long-distance movements for most birds (e.g., a 50-km threshold was overly sensitive, and 200-km threshold missed some long-distance movements). We grouped together any consecutive days of long-distance movement or stationarity (i.e., any days not identified as long-distance movements) and considered each of these to be a separate stationary or movement period. We then assigned each stationary period to one of three types—winter, summer, and stopover—and each movement period as either seasonal migration or a within-season movement using the following criteria:

1. Winter periods were defined as stationary periods lasting at least 30 days and meeting at least one of the following criteria: (a) having a maximum net displacement of less than 100 km (i.e., within 100 km of the 31 December reference point); (b) occurring entirely within the months of December and January; or (c) containing at least three of the months between September and March (inclusive).
2. Summer periods were defined as stationary periods lasting at least 30 days that occurred at least partially in the months of June–August (inclusive).
3. We then assigned any remaining stationary periods (i.e., shorter than 30 days or not meeting the other criteria above) as winter, summer, or stopover depending on whether they fell within or between defined winter and summer periods.
4. We classified periods of movement as either within-season movements or migration. We considered a movement to be a within-season movement if it linked two wintering or two summer periods and to be a migration if it linked periods of different types (e.g., winter/summer, winter/stopover), or if it connected two stopover sites.

We used these classifications at the daily scale to classify each original GPS or PTT fix, which accounted for differences in diurnality among species and increased the precision of our estimates of migration timing to hours rather than days. For migration periods, we verified whether a bird was migrating for the first and last fixes of a calendar day; a fix was classified as migration if

its net displacement relative to the previous fix was in the net daily direction of movement. If it was not, the fix was assigned the class of the previous or subsequent calendar day. For example, for spring migration, a fix would be classified as migration if its net displacement was greater than that of the preceding fix. Finally, we verified all classifications manually using a combination of plots of net displacement over time and maps of classified locations and reassigned any points that were incorrectly classified; these were primarily long stopovers (>30 days) at the beginning of spring migration in northeastern California (Miller et al., 2005).

Using these segmented paths, we identified the start date of spring migration in the first year of tracking for all birds tagged during winter. The spring migration departure date was the first date a bird was detected on its spring migration, spring stopover, or summer area in a calendar year, whichever was earliest. For example, a spring stopover location would be used as the start date for spring migration if no fixes were available between departure from the wintering grounds and arrival at the stopover site. We excluded one individual that had a long monitoring gap between the last detection in a wintering period and the first detection in another season (92 days without fixes), so it was not possible to identify its migration date; all other individuals had monitoring gaps of less than 10 days, with most being less than one day. All spring migrations began ≥13 days after transmitter attachment (mean: 135 days) and ≥47 days after surgery for birds with surgically implanted transmitters, which is beyond the expected duration of any effects of capture or surgery on movement (Garrettson et al., 2000; Kesler et al., 2014; Lamb et al., 2020).

We also calculated the duration of each bird's first stopover, based on evidence that LPAIV infection affected swans' stopover behavior (van Gils et al., 2007). We focused on the first stopover because it was the closest to the date of sampling and because transmitters sometimes failed prior to arrival at the breeding grounds, thus limiting our ability to identify stopovers later in migration for some individuals. For birds that were not observed stopping over on migration, we imputed a stopover duration of zero days if there was no more than a four-day monitoring gap during the migration period ($n = 5$); we selected four days as a conservative cutoff because it was below the lower quartile of stopover duration for any species.

We used linear models to examine the relationship between migration phenology and infection status. We modeled the spring migration departure day (day of year: 30–139) as a function of influenza infection status at the time of capture, species, and the interaction between infection status and species. We modeled the duration of the first stopover (in days) as a function of influenza infection status at the time of capture, species, their interaction, and the start date of spring migration. We built two different models for each response variable: one that included active influenza infection status based on rRT-PCR results and one that included prior influenza infection status based on bELISA results (i.e., detection of influenza antibodies). We also tested linear mixed-effects models that included calendar year as a random intercept to account for nonindependence of migration timing within years (e.g., due to social behavior or differences in weather). The quantitative results from these mixed-effects models were practically identical to those from the linear models without year; the random intercept of year explained almost no variance; and adding the random effect of year did not improve model fit. Therefore, we present only the linear models without a random intercept for year.

From each model, we calculated pairwise differences between infected and uninfected birds within each species to infer evidence for relationships between infection and migration timing. We did not establish a threshold for statistical significance but instead reported 95% confidence intervals (CIs), p values, and the strength of statistical evidence following guidelines from Muff et al. (2021). We also calculated a conservative estimate of the contribution of infection status to the explanatory power of each model by calculating the reduction in R^2 (i.e., variance explained) when infection status and its interaction with species were removed from each model. All data processing and analyses were performed in R version 4.0.3 (R Development Core Team, 2020), using the packages glmmTMB version 1.1.2 for fitting mixed-effects models (Brooks et al., 2017), DHARMa version 0.4.3 for assessing model fit (Hartig, 2019), and emmeans version 1.6.3 for pairwise contrasts (Lenth, 2021).

Local movements

We studied space use shortly after sampling in canvasbacks, pintails, and mallards to compare local movement behavior of actively infected birds with those that were uninfected; greater white-fronted geese were excluded because active infection data were unavailable and antibody data were not used in this analysis. We analyzed daily movement patterns within 12 days of capture, to evaluate how movements changed over time between infected and uninfected birds from the point of capture through presumed recovery (given that influenza infection is expected to last 5–10 days in waterfowl; Hénaux et al., 2010). We expected that, if active influenza infection affected local movement behavior, movement patterns would differ between infected and uninfected birds in the

first few days following sampling, but any infection-induced differences in movement would disappear by the end of 12 days, when birds have presumably recovered from infection. More individuals were included in this analysis than in the migration analysis since some transmitters failed prior to the initiation of spring migration or had gaps in data that precluded estimating migration timing.

To measure space use at the daily scale, we used three related metrics of local movement: the area of a daily 100% minimum convex polygon (MCP), the total daily distance moved, and the maximum daily displacement. Daily MCPs draw a convex hull around all daily locations; this metric represents an individual's degree of exploration (Bengtsson et al., 2014; Spiegel et al., 2017) and has previously been used to analyze duck responses to influenza infection (Bengtsson et al., 2016). Total daily distance moved is the sum of all distances between GPS fixes in a day; it differs from MCP area because it measures movement rather than space use (e.g., commuting behavior can increase distance moved without increasing space use). Maximum daily displacement is the maximum pairwise distance between any two GPS fixes in a day and has also been used in a prior analysis of influenza in ducks (Bengtsson et al., 2016).

We resampled telemetry data to 30-min intervals (i.e., no more than one GPS fix every 30 min, but up to 13 h between fixes during low-frequency data collection), then calculated each movement metric per individual per day. We split days at sunrise because waterfowl movements tend to peak at dawn and dusk (Bengtsson et al., 2014; McDuie, Casazza, Overton, et al., 2019), so using sunrise as the beginning of a day ensures that nighttime foraging movements are included as part of the same day. Sunrise times were identified using the suncalc package version 0.5.0 (Thieurmel & Elmarhraoui, 2019), and MCPs were fitted using the amt package version 0.1.4 (Signer et al., 2019). We filtered the data set to include only bird days that had GPS fixes representing at least 6 h of the day; visual inspection of the relationship between number of hours of monitoring and each of the movement metrics showed that these relationships reached an asymptote around 6 h (and that the number of hours was more closely related to each movement metric than was the number of fixes). We also included only birds with at least three days of data over the 12-day period. This filtering removed all birds with PTTs.

For each of the three movement metrics (MCP area, total distance moved, and maximum displacement), we built a linear mixed-effects model with log-transformed area or distance as the response variable. Explanatory variables were: active influenza infection status (as determined by rRT-PCR); species; days since influenza sampling (to measure changes in movement as a result of capture effects, weather, or seasonality); sex; all pairwise interactions with species (to account for interspecific differences in the effect of infection, sex, and days since sampling on space use); the pairwise interaction between active infection status and days since sampling (to test the hypothesis that movement changes as birds recover from infection); and a three-way interaction among active infection status, days since sampling, and species. We log-transformed days since sampling because we hypothesized that differences in movement between infected and uninfected birds would be largest in the first few days following sampling (Bengtsson et al., 2016). We included log-transformed number of GPS fixes as a fixed effect to account for the sensitivity of movement metrics to sample size. We also included a unique identifier for each individual as a random intercept to account for inter-individual variation in space use that was unrelated to infection. To understand the explanatory power of the fixed and random effects in the model, we calculated marginal and conditional R^2 values using the performance package version 0.8.0 (Lüdecke et al., 2021). We also used the emmeans package (Lenth, 2021) to test for differences in space use or movement distances between infected and uninfected birds at each day (1–12) following sampling by calculating pairwise differences and 95% CIs of this difference between groups.

RESULTS

Prevalence of active influenza infection (i.e., a positive rRT-PCR assay, $Ct \leq 45$) was 7% in canvasbacks ($n = 4/54$), 11% in mallards ($n = 3/27$), and 6% in northern pintails ($n = 4/70$). Influenza antibody prevalence (i.e., a positive bELISA, S:N ratio <0.5) was 79% in canvasbacks ($n = 37/47$), 38% in northern pintails ($n = 8/21$), and 58% in greater white-fronted geese ($n = 7/12$). Active infection data were unavailable for greater white-fronted geese, and antibody data were unavailable for mallards.

Migration timing

We identified spring migration departure dates for 84 adult migrants from the three migratory species: 31 canvasbacks ($n = 2$ infected, $n = 22$ with antibodies), 41 northern pintails ($n = 3$ infected, $n = 7$ with antibodies), and 12 greater white-fronted geese ($n = 7$ with antibodies) (Figure 1; Appendix S1: Figure S2). Departure dates for spring migration varied widely within and among species, from 31 January to 20 May (Figure 1; Appendix S1: Figure S3).

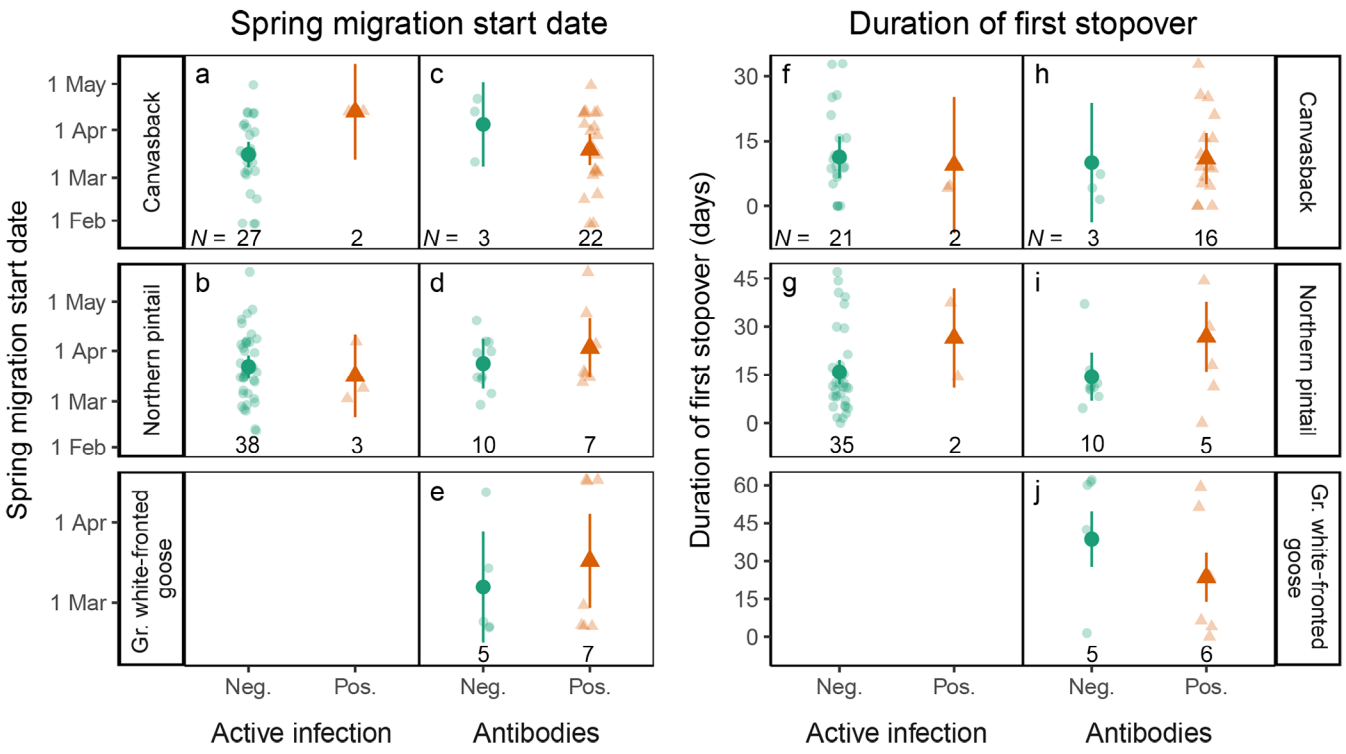

FIGURE 1 Spring migration departure date (a–e) and duration of first stopover (f–j) by species and infection status across 84 individuals with paired influenza and telemetry data. Partially transparent points show raw data; large points and error bars show means and 95% confidence intervals estimated from linear models. Each column shows results from a separate linear model (a, b: Appendix S1: Table S1; c–e: Table S3; f, g: Table S5; h–j: Table S4). For stopover duration (f–j), this model also accounts for migration start date, and model means represent an individual with the median departure date (23 March). Individual birds were assessed for active infection (viral RNA detection via real-time reverse transcriptase-polymerase chain reaction) and/or prior influenza exposure (antibody serostatus via blocking enzyme-linked immunoassay); active infection data were unavailable for geese. Numbers at the bottom of each panel indicate sample sizes for each species, movement metrics, and influenza infection/exposure status combination. Gr., greater; Neg., negative; Pos., positive.

There was weak evidence that canvasbacks that were actively infected at the time of capture initiated migration later than their uninfected counterparts (Figure 1a; Appendix S1: Tables S1 and S2); the mean spring migration departure date was 16 March for uninfected canvasbacks (day 75; $n = 27$), compared to 14 April for infected canvasbacks (day 103; $n = 2$), a difference of 28 days (95% CI: 4 days earlier to 60 days later; $t(66) = 1.729$, $p = 0.088$). We detected no evidence for a relationship between active infection status at capture and migration departure date for pintails (Figure 1b; Appendix S1: Tables S1 and S2) or for a relationship between antibody status and migration departure date in any species (Figure 1c–e; Appendix S1: Tables S2 and S3). The full model using active infection status explained 5% of the variation in spring migration departure dates; a model with species alone explained 0.7% of the variation, indicating that active infection status and its interaction with species explained the remaining 4.3%. For antibody status, the full model explained 10% of the variation in spring migration departure dates, of which antibody status and its interaction with species explained about half (4.6%).

We also calculated the duration of the first spring stopover for 72 migrants: 23 canvasbacks ($n = 2$ infected, $n = 16$ with antibodies), 37 northern pintails ($n = 2$ infected, $n = 5$ with antibodies), and 11 greater white-fronted geese ($n = 6$ with antibodies). The duration of the first stopover was related to departure date in all three species, such that individuals that departed later made a shorter first stopover (Appendix S1: Table S4). After accounting for departure date, there was weak evidence that stopover duration was related to antibody status in northern pintails (Figure 1i; Appendix S1: Table S4); on average, pintails with antibodies to influenza stopped over for 12 days longer than pintails without antibodies (95% CI: difference of 0–24 days; $t(38) = 1.906$, $p = 0.064$). In contrast, for greater white-fronted geese, we found moderate to weak evidence that birds with antibodies to influenza made a first stopover that was on average 15 days shorter than those without antibodies (95% CI: difference of 1–29 days; $t(38) = -2.101$, $p = 0.042$; Figure 1j). We detected no evidence for a

relationship between active infection status and stopover duration in pintails or canvasbacks or for a relationship between antibody status and stopover duration in canvasbacks (Figure 1f–h; Appendix S1: Tables S4 and S5). The full model using active infection status explained 23% of the variation in stopover duration; a model with species and migration start date alone explained 20% of the variation, indicating that active infection status and its interaction with species explained the remaining 3%. For antibody status, the full model explained 64% of the variation in spring migration departure dates, with antibody status and its interaction with species explaining about 8%.

Local movements

We measured local movement behavior in the days immediately following sampling for canvasbacks ($n = 48$, 4 infected), mallards ($n = 27$, 3 infected), and northern pintails ($n = 62$, 4 infected). All three movement metrics (MCP area, total daily distance moved, and maximum daily displacement) were correlated ($r > 0.92$ for log-transformed variables) and produced qualitatively similar results (Figure 2; Appendix S1: Figures S4 and S5 and Tables S6–S8); we present results for MCPs here. Birds that tested positive for active influenza infection tended to use smaller areas than uninfected birds, particularly for canvasbacks and pintails in the first few days following sampling (i.e., the period when they were most likely to be actively infected; Figure 2a,b). For example, on the first day following sampling, our model predicted that an infected pintail would use an area 7.6 times smaller than an uninfected pintail (0.007 km^2 vs. 0.056 km^2; $t(1368) = 2.36$, $p = 0.018$; Appendix S1: Table S6). Space use increased with time since capture for pintails and canvasbacks regardless of infection status, likely indicating capture effects, but this increase was stronger for infected than for uninfected birds. For example, the model predicted that a pintail that was actively infected at the time of sampling would increase its daily space use from 0.020 km^2 (95% CI: 0.004–0.101) on the first day following sampling to 0.600 km^2 (95% CI: 0.128–2.815) on day 12 (a 30-fold increase; $t(1368) = 2.827$, $p = 0.0048$). There was no evidence for a relationship between space use and active infection status in mallards (Figure 2c) or for changes in space use over time in mallards, but male mallards used larger areas than females (Appendix S1: Table S6). The full model explained 29.4% of the variation in MCP area, approximately half of which was attributed to individual-level effects (marginal $R^2 = 0.16$). A model without infection variables explained 28.9% of the variation in MCP area, indicating that 1.5% of the variation in MCP area was explained by active infection status and its interactions.

DISCUSSION

For four waterfowl species inhabiting California's Central Valley and San Francisco Bay Estuary, relationships

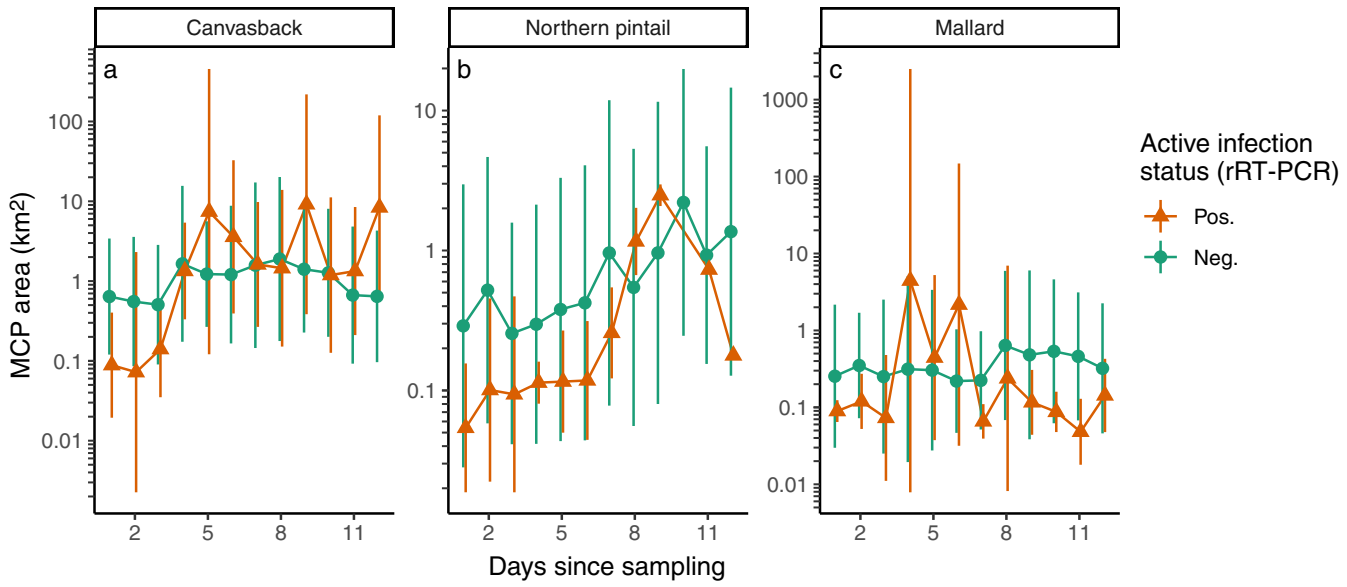

FIGURE 2 Space use by active infection status, species, and days since sampling. Space use was measured using the area of a minimum convex polygon (MCP) that encloses all the points used by an individual on one day. Points and lines show geometric means and one standard deviation of the mean. Sample sizes differ between days because data were not sufficient to estimate space use for every individual across the entire period. For other movement metrics, see Appendix S1: Figures S4 and S5. Neg., negative; Pos., positive; rRT-PCR, real-time reverse transcriptase-polymerase chain reaction.

between avian influenza infection and movement varied among species, movement metrics, and measurements of influenza infection. Northern pintails with antibodies to influenza, indicative of prior infection, made stopovers 12 days longer than those with no evidence of prior infection, but this pattern was reversed in greater white-fronted geese, where previously infected geese made shorter stopovers (15 days), and was absent in canvasbacks. We also found some evidence for a 28-day delay in spring migration departure in canvasbacks that were actively infected on their wintering grounds, despite low infection prevalence ($n = 2$ infected canvasbacks). In addition, pintails and canvasbacks with active influenza infections used smaller areas than uninfected birds while on their wintering areas (7.6 and 4.9 times smaller on the first day following sampling, respectively), but we found no evidence for altered movements in infected mallards during the breeding season. Together, these results highlight that the relationships between infection and movement behavior can be species-specific, context-dependent, and occur at multiple time scales, but that the effect sizes of these relationships can be large where they are present.

Our finding that infected canvasbacks and pintails used smaller areas during the period of presumed active influenza infection (within six days of sampling) suggests that infection-induced changes in movement behavior could limit local dispersal of influenza and could affect bird health by limiting foraging opportunities. Infected birds sometimes used areas an order of magnitude smaller than their uninfected counterparts; this infection-associated decrease in movement lasted only a few days but could still reduce pathogen spread between habitat patches and/or increase environmental loads of influenza virions, especially if it occurs during the peak shedding period (~days 1–5 of infection; Arsnoe et al., 2011; Shriner et al., 2021). These patterns also suggest that influenza infection could have a short-term energetic cost that causes a sickness behavior (Lopes et al., 2021). Reducing long distance flights between patches could help offset the energetic costs of mounting an immune response (van Dijk et al., 2015), especially since flight is energetically demanding (Norberg, 1996). Although reducing flight could also limit a bird's ability to obtain food (Binning et al., 2017), changes in habitat conservation and agricultural practices in the Central Valley have increased habitat availability for waterfowl and decreased distances between roosts and feeding sites (Ackerman et al., 2006; Fleskes et al., 2018; McDuie, Casazza, Overton, et al., 2019), which could allow birds to adjust their movement behavior to compensate for their infection status and energetic state. However, we detected no relationship between space use and infection in mallards, which were sampled during the breeding season. Breeding-season movements are constrained by nesting behavior, especially for females (Croston et al., 2021; Eichholz & Elmberg, 2014), so infection might have limited effects on movement during the summer. Local processes are among the most important drivers of large-scale patterns of influenza infection in wild waterfowl (Gorsich et al., 2021), and longer waterfowl residence times are associated with influenza outbreaks in poultry (Humphreys et al., 2020); therefore, these results indicate that any infection-related reductions in local movements could affect both local and large-scale viral dispersal.

Infection-related changes in migration phenology, which have been observed for avian influenza (van Gils et al., 2007), avian blood parasites (DeGroote & Rodewald, 2010), and in other non-avian taxa (Halttunen et al., 2018; Mysterud et al., 2016), are usually attributed to an energetic cost of infection (DeGroote & Rodewald, 2010). Although the patterns we observed differed among species and infection metrics, the relationships of migration departure dates and stopover duration with infection could be consistent with a lasting energetic cost of infection. For example, longer stopovers and delayed migration, which we observed in pintails and canvasbacks, respectively, are both consistent with expectations of a negative relationship between movement propensity and energy stores (Schmaljohann & Eikenaar, 2017). These results also support previous findings in Bewick's swans, where infected birds exhibited reduced feeding rates, delayed migration, and shorter movement distances, even one month after infection (van Gils et al., 2007). In contrast, greater white-fronted geese with antibodies to influenza often skipped a traditional stopover site in northern California, but most geese migrated up the Pacific coast to Alaska within days of one another (Appendix S1: Figure S3). These patterns could indicate that shorter stopovers allow birds to compensate for a later departure (Nilsson et al., 2013), possibly making up for energetic losses earlier in the winter season. Differential use of these stopover sites in northern California and southern Oregon has previously been observed across geese with similar migration destinations (Ely & Takekawa, 1996), but to our knowledge has never before been linked to physiological states (i.e., antibody status). Although the patterns we observed manifested differently across species, all could indicate an energetic cost of influenza infection, which could have carryover effects for reproductive propensity and success (Buehler et al., 2010).

In addition to an energetic cost of infection, relationships between movement patterns and infection status could stem from correlations among behavior, habitat use, and influenza exposure. For example, birds that migrate together (e.g., in family or social groups) will have similar migration phenology and pathogen exposure, potentially producing correlations between the two that are not

causal. Juvenile ducks tend to complete spring migration later than older adults (Newton, 2011) and are more likely to be infected with influenza (Olsen et al., 2006), which could produce movement–infection relationships. However, all migrants analyzed in this study were >1 year of age, so this effect was probably not an important driver of the patterns in our data. Similarly, space use and infection could each independently stem from habitat use. For instance, individuals using habitats with high food availability might need less space (Ringelman et al., 2015; Saïd et al., 2009); if these resource-rich habitats also support high waterfowl densities (Gilmer et al., 1982) and therefore a large environmental reservoir of influenza viruses (Ramey et al., 2020; Ramey, Reeves, et al., 2022), habitat use could produce an apparent relationship between space use and infection. Finally, most birds were sampled weeks or months before migration, leaving their infection statuses during migration unknown. Longitudinal studies that resample individuals (Tolf et al., 2013; Trovão et al., 2021) could help clarify the causal nature of these relationships as well as how infection interacts with stressors such as habitat availability and environmental contamination (Teitelbaum, Ackerman, et al., 2022). Regardless of the mechanism driving infection–movement relationships, these associations can alter the expected dynamics of infection prevalence by affecting contact patterns between individuals, environmental exposure, and the role of birds as dispersal vectors.

We found relatively large effect sizes (e.g., migration delay of 28 days for infected canvasbacks) but also substantial variation in movement behavior and its relationship to active or prior infection, both between and within species. Within species, the variation we observed could be primarily biological (i.e., due to unmeasured variables such as nutritional status or differences among viral strains causing infection) or statistical (i.e., due to uncertainty in parameter estimates stemming from low infection prevalence). Between species, this variation suggests that each taxon has a different biological relationship with influenza, for example, due to differences in their physiological and immunological responses to influenza infection. Antibody prevalence was higher in greater white-fronted geese than in pintails (Hill et al., 2010, 2012; this study), which can be a sign of tolerance to infection (Miller et al., 2006) and could therefore partially explain why goose and pintail stopover behavior had divergent associations with influenza infection history. Similarly, canvasbacks and other diving ducks tend to have low prevalence of active infection but high antibody prevalence (Ferro et al., 2010; Hill et al., 2010; Stallknecht & Shane, 1988; this study), which can stem from a short duration of infection relative to the period of antibody detection (Hall et al., 2015). We observed that infection had a relatively fleeting effect on canvasback space use, which would be consistent with a short duration of infection. Cross-species differences in infection–movement relationships can stem from multiple mechanisms, including variation in infection duration, tolerance, and seasonality across species (Adelman & Hawley, 2017; Sánchez et al., 2018).

The epidemiology of avian influenza is complex, making studying its ecology in the field particularly challenging. Researchers must contend with multiple co-circulating subtypes, partial cross-immunity (Webster et al., 1992), uncertainty in the duration of immunity (Lisovski et al., 2018), seasonality in infection prevalence (Munster et al., 2007), and a relatively short infectious period that varies depending on exposure routes, doses, and viral strains (Brown et al., 2006; Hénaux et al., 2010). Together, these factors can result in low infection prevalence among sampled birds, making it difficult to statistically compare infected and uninfected groups (Hill & Runstadler, 2016; van Gils et al., 2007). Future studies of movement behavior that focus on high-prevalence periods, such as autumn migration (Munster et al., 2007; van Dijk et al., 2014), and more susceptible groups, such as juveniles (van Dijk et al., 2014), would help further our understanding of how avian influenza affects migratory waterfowl across the annual cycle. In this study, we resampled only one individual (mallard 180627.2); this bird tested positive for active influenza infection 13 days apart, which could stem from a long infectious period, infections with different strains, or viral detection after recovery from infection. This myriad of hypotheses emphasizes the need for high-resolution information on avian influenza infection among wild bird hosts from multiple species and geographic areas to fully understand how influenza infection affects host behavior and movement.

Avian influenza poses an ongoing management challenge for poultry producers and an emerging threat to wildlife health (Ramey, Hill, et al., 2022), but predicting its spread and dynamics remains difficult. Understanding how influenza infection affects wild birds is particularly important in the context of ongoing outbreaks of HPAIV in North America, Eurasia, and Africa, where wild bird mortality has been significant but where impacts still vary greatly across species and flyways (Lean et al., 2022; Prosser et al., 2022). In combination with laboratory studies across species (e.g., Brown et al., 2006; Curran et al., 2013), observational field studies will help clarify the mechanisms that drive observed patterns of influenza infection in wildlife and ultimately help predict when and where AIV epidemics are most likely to occur. Beyond the avian influenza system, these results also highlight the value of studying diverse host species for understanding the ecology of multihost pathogens.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Teitelbaum, Casazza, et al., 2022) are available from the U.S. Geological Survey ScienceBase repository: https://doi.org/10.5066/P97NEY5Y. Code (Teitelbaum, 2022) is available from Zenodo: https://doi.org/10.5281/zenodo.7076254.

ETHICS STATEMENT

Capture, banding, and marking were carried out under U.S. Geological Survey (USGS) Bird Banding Permits 21142 and 22911, U.S. Fish and Wildlife Service Migratory Bird Permit MB-102896, and California Scientific Collecting Permits SC-003855 and SC-8090. Capture and marking were approved by the USGS-Western Ecological Research Center Animal Care and Use Committee.

ORCID

Claire S. Teitelbaum https://orcid.org/0000-0001-5646-3184
Michael L. Casazza https://orcid.org/0000-0002-5636-735X
Fiona McDuie https://orcid.org/0000-0002-1948-5613
Susan E. W. De La Cruz https://orcid.org/0000-0001-6315-0864
Cory T. Overton https://orcid.org/0000-0002-5060-7447
Laurie A. Hall https://orcid.org/0000-0001-5822-649X
Elliott L. Matchett https://orcid.org/0000-0001-5095-2884
Joshua T. Ackerman https://orcid.org/0000-0002-3074-8322
Andrew M. Ramey https://orcid.org/0000-0002-3601-8400
Diann J. Prosser https://orcid.org/0000-0002-5251-1799

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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