



Capture height biases for birds in mist-nets vary by taxon, season, and foraging guild in northern California

Los sesgos en la altura de la captura de aves con redes de niebla varía por taxón, estación y gremio de forrajeo en el norte de California

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ABSTRACT. Mist-netting is a widely used technique for capturing birds to estimate abundance, demography, and population trends. Investigators in most studies use primarily or only ground-level mist-nets that extend < 3 m vertically. Therefore, data analyses require assumptions that the degree to which birds of interest occupy unsampled vertical space is unrelated to variables of interest, e.g., age structure, sex ratio, arrival and departure dates, and probability of recapture. Despite the widespread use of analyses based on these assumptions, they have rarely been tested. We analyzed capture data from paired ground-level and elevated (~3–5 m above the ground) mist-nets from 1993 to 2020 at Coyote Creek Field Station in Milpitas, CA, USA. Because capture height biases are driven by behavior, we expected that they may vary by net location, foraging guild, capture history, age, sex, and season. We built binomial models in a Bayesian framework to analyze the effects of these variables. Of 43 taxa, 13 were biased toward capture in elevated nets and seven toward capture in ground-level nets. These biases showed little variation among three net locations. Capture height biases were largely consistent with the documented heights of different foraging guilds. In one taxon, recaptured birds were more likely to be captured in elevated nets, possibly because of net avoidance or differences between overwintering and transient individuals. Only one taxon each exhibited either a sex or age effect on capture height. We found seasonal patterns in capture height for five taxa including residents and short- and long-distance migrants. Our results demonstrate that capture height biases were present at our research site and that the standard practice of deploying only ground-level nets may bias data in ways not generally recognized. Further study of these biases could improve mist-netting methods and increase the value of bird banding data.

RESUMEN. La captura de aves con redes de niebla es una técnica ampliamente utilizada para estimar la abundancia demografía y tendencias poblacionales. En la mayoría de los estudios, los investigadores utilizan redes de niebla al nivel del suelo que se extienden < 3 m verticalmente. Por lo tanto, el análisis de datos requiere de supuestos como que el grado en el cual las aves de interés ocupan el espacio vertical no muestreado no se encuentra relacionado con las variables de interés, e.g., estructura de edad, la proporción de sexos, fechas de llegada y de partida y probabilidad de recaptura. A pesar del uso común de los análisis que se basan en dichos supuestos, estos raramente han sido puestos a prueba. Analizamos datos de captura con redes de niebla pareadas a nivel del suelo y elevadas (~3–5 m por encima del suelo) entre 1993 y 2020 en la estación de campo de Coyote Creek en Milpitas, CA, EEUU. Debido a que los sesgos en la altura de la captura están determinados por el comportamiento, esperamos que estos pueden variar por la ubicación de la red, gremio de forrajeo, historia de capturas, edad, sexo y estación. Construimos modelos binomiales en un marco Bayesiano para analizar los efectos de estas variables. De los 43 taxones, 13 estuvieron sesgados hacia la captura en redes elevadas y siete hacia la captura en redes a nivel del suelo. Los sesgos en la altura de captura fueron mayormente consistentes con las alturas documentadas para los diferentes gremios de forrajeo. En un taxón, fue más probable recapturar los individuos en redes elevadas, posiblemente debido a que evitan las redes o a diferencias entre individuos que pasan el invierno y los que son transitorios. Solo un taxón, mostro cada uno, efectos del sexo o la edad sobre la altura de la captura. Encontramos patrones estacionales en la altura de la captura para cinco taxones incluyendo residentes y migrantes de corta y larga distancia. Nuestros resultados demuestran que los sesgos en la altura de la captura estuvieron presentes en nuestro sitio de investigación y que una practica estandarizada de utilizar solo redes de niebla a nivel del suelo puede sesgar los datos en formas que no son reconocidas generalmente. Estudios futuros sobre los sesgos pueden mejorar los métodos basados en redes de niebla e incrementar el valor de los datos de anillamiento de aves.

Key Words: *bird banding; elevated mist-net; near-passerines; passerines; population monitoring; sampling bias*

INTRODUCTION

Mist-nets are widely used to survey bird presence, abundance, and survival (Dunn and Ralph 2004), for example at bird banding stations (Spotswood et al. 2012) and in the Monitoring Avian Productivity and Survivorship (MAPS) and el Monitoreo de Sobrevivencia Invernal (MoSI) Programs (DeSante et al. 1999, DeSante and Kaschube 2009). Common, widely used mist-net deployment methods facilitate comparability between datasets collected by different researchers (Karr 1981, Remsen and Good

1996, DeSante et al. 2020). That consistency, however, amplifies the risk of bias because the broad usage of a method may cause any biases inherent to that method to be replicated across many datasets, potentially leading to large errors (Dufour and Weatherhead 1991, Remsen and Good 1996, Larsen et al. 2007, Bonter et al. 2008). Mist-netting data can underlie population trend detection, range shift monitoring, species assemblage detection, the design and evaluation of conservation strategies, and other important ornithological goals (Dunn and Ralph 2004).

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Any biases in mist-net data may therefore have far-reaching consequences; and as Biro and Dingemanse (2009:66) observe, “most sampling techniques possess inherent sampling inefficiency and bias.”

Mist-netting avoids some biases present in other survey methods: compared to visual or aural surveys, mist-netting is less likely to miss small, quiet, and secretive species (Wang and Finch 2002, Dunn and Ralph 2004) and likely depends less upon the field identification skills of individual researchers (Karr 1981). However, mist-nets may not capture a representative sample of the local avifauna for several reasons. For example, (1) variable external conditions may impact capture rates (e.g., rainfall, Silkey et al. 1999; vegetation, Pagen et al. 2002, Wang and Finch 2002); (2) species vary in their capturability (MacArthur and MacArthur 1974, Silkey et al. 1999, Wang and Finch 2002); (3) sex, feeding strategy, or personality may drive inter-individual differences in capturability (Dufour and Weatherhead 1991, Vanderkist et al. 1999, Biro and Dingemanse 2009); and (4) individuals may vary over time in their susceptibility to capture due to changes in age, condition, molting status, status as a territory-holder or a transient, or previous capture experience (MacArthur and MacArthur 1974, Fitzgerald et al. 1989, Dufour and Weatherhead 1991, Domènech and Senar 1997, Insley and Etheridge 1997, Bart et al. 1999, Silkey et al. 1999, Nur et al. 2004, Marques et al. 2013, Roche et al. 2013, LaBarbera and Scullen 2021). Quantifying potential biases such as these allows researchers to consider them when designing studies and interpreting data, and to eliminate or moderate their impacts on study results (Biro and Dingemanse 2009). There is, however, an additional potential bias in mist-netting that has thus far been studied little, rendering it difficult for researchers to account for: capture height bias.

Mist-nets are commonly set only at ground-level, where they capture birds no higher than ~3 m above the ground (Bonter et al. 2008, Vecchi and Alves 2015). Methods for achieving alternative net heights exist, e.g., Stokes et al. (2000), but appear to be rarely used. Mist-net height is such a consistent aspect of standard procedure that it goes generally unremarked; for example, in the widely used MAPS Manual, net height is only briefly mentioned (DeSante et al. 2020). However, concerning, Remsen and Good (1996) demonstrated that even slight differences in the vertical activity patterns of birds could result in considerable differences in capture rate, as the birds became more or less likely to fly over rather than into the net. Because these vertical activity patterns are relative to the top of the net, even small differences in net height could produce differences in capture patterns.

Available evidence suggests that net height does influence capture patterns. It has been documented that ground-level mist-nets alone fail to adequately assess community composition, as they bias samples toward understory-favoring species (Fitzgerald et al. 1989, Remsen and Good 1996, Wang and Finch 2002, Derlindati and Caziani 2005, Bonter et al. 2008). For example, in the forest of Orongorongo Valley, New Zealand, height biases were found in 7 of 14 species captured in net rigs spanning 1.5–13.5 m above the ground (Fitzgerald et al. 1989). In the Atlantic rainforest of Ilha Grande, Brazil, “vertically-mobile” mist-nets that were positioned 0–17 m above the ground captured nearly 50% more species than standard ground-level mist-nets and

resulted in an estimate of species richness nearly twice that of ground-level nets (Vecchi and Alves 2015). In NY state, USA, mist-nets elevated to ~3 m above ground level during migration captured 12 species not captured in ground-level nets, and > 50% of species were more likely to be captured at one net height than the other, with more species captured in ground-level nets (Bonter et al. 2008).

The results of these studies underscore the need to better understand the effects of mist-net height on capture patterns. They demonstrate that net height matters in different habitats (rainforest with a mean canopy height of 23 m vs. early secondary-growth habitats with mean vegetation heights of 5 m), species assemblages (tropical vs. temperate and mainland vs. island avifauna), and life history periods (tropical winter vs. temperate migrations), and that the specific effects of mist-net height on capture patterns vary with at least some of these variables (Fitzgerald et al. 1989, Bonter et al. 2008, Vecchi and Alves 2015). To understand the possible biases in data collected using only ground-level nets, research in other habitats and during more life history periods is needed. Crucially, it is not well-studied whether ground-level nets introduce biases into uses of banding data other than characterizing community composition, such as demographic studies, migration phenology, and population trends, although theoretical analysis suggests that they may (Remsen and Good 1996).

It is important to understand not only how sampling height impacts captures generally, but specifically how those impacts differ among species, individual attributes, and external conditions, so that researchers can determine whether sampling height may affect their specific research question. We expect that capture height bias will vary with other factors because capture height biases should be driven by avian behavior (MacArthur and MacArthur 1974, Remsen and Good 1996), which can vary by age, sex, personality, experience, territorial vs. non-territorial status, foraging guild, weather, and many other factors (Bart et al. 1999, Silkey et al. 1999, Nur et al. 2004, Marques et al. 2013, Roche et al. 2013, LaBarbera and Scullen 2021). Such interactions have been documented in comparisons of capturability among different trap types, where, for example, different trapping methods may capture different age or sex ratios (Dufour and Weatherhead 1991, Domènech and Senar 1997). These effects can interact with yet additional factors, as when abundance estimates vary both with trap type and habitat (Pagen et al. 2002, Wang and Finch 2002), and when Insley and Etheridge (1997) observed that mist-nets under-captured adult Redshanks *Tringa totanus* relative to juveniles, but only in early autumn, because of age-specific molt phenology. The few data that exist on mist-net capture height biases support the existence of these interactions: multi-species studies found instances of the effect of mist-net height on capture probability interacting with foraging guild (Vecchi and Alves 2015), time of day, season, capture history (Fitzgerald et al. 1989), age, and sex (Bonter et al. 2008).

We examined a year-round, 26-year capture dataset from riparian woodland in the temperate Mediterranean climate of the south Bay Area, California, USA, to test for differences in avian capture probabilities between paired ground-level mist-nets and mist-nets elevated ~3 m above ground level. We further explored whether capture height bias interacted with species, capture history, age,

Table 1. Summary of ground-level and elevated captures among three paired net rigs at the Coyote Creek Field Station, Milpitas, CA, USA. Net sites were identified by their distance (in meters) upstream from the entrance of the Coyote Creek into the San Francisco Bay. Nets 9280 and 9590 were operated once weekly on Saturdays and Sundays, respectively, year-round. Net 8735 was operated on multiple days each week only for the beginning of the study. Although the elevated nets captured slightly more birds at all three locations, this difference was not significant.

Net Site ID	Years of Operation	Number of Ground-level Captures	Number of Elevated Captures	Probability of Ground-level Capture 95% CI
8735	1993–1998	580	591	0.467–0.524
9280	1993–2020	1456	1545	0.468–0.503
9590	1993–2020	1546	1594	0.475–0.510

sex, foraging guild, net location, and season. To our knowledge, this work represents the first test of a relationship between foraging height and capture height bias and the largest exploration of capture height biases across the full annual cycle.

METHODS

We used constant-effort bird banding data from Coyote Creek Field Station (hereafter CCFS) in Milpitas, CA, USA, from 1993 to 2020. CCFS is located at the southern end of the San Francisco Bay (37.4381°N, 121.9285°W). The 12-ha area is divided among four habitats: a remnant riparian corridor that borders the creek, two areas of restored riparian woodland (replanted in 1987 and 1993, respectively), and a large grassy area that is managed as an overflow channel for flood control. Although ground-level mist-nets were operated in all these habitats, elevated mist-nets were operated only in the remnant riparian habitat. Within 5 m of the mist-nets, the dominant overstory plant species were box elder (*Acer negundo*), western sycamore (*Platanus racemosa*), Fremont cottonwood (*Populus fremontii*), and California buckeye (*Aesculus californica*), and the dominant understory plant species were coyote brush (*Baccharis pilularis*), California blackberry (*Rubus ursinus*), and poison hemlock (*Conium maculatum*). Vegetation surveys conducted in 1997, 2005, and 2013 found no changes over that time in the remnant riparian habitat in understory abundance or diversity, overstory abundance or diversity, tree height, tree diameter-at-breast-height, or canopy cover (San Francisco Bay Bird Observatory, unpublished data).

Constant effort mist-netting

Three net arrays, composed of 14, 14, and 19 mist-nets, were operated on Wednesdays, Saturdays, and Sundays, respectively, year-round. Most of the nets in these regularly operated net arrays were standard ground-level nets; however, there were also two paired net rigs with two nets stacked on top of each other (one ground-level and one elevated), with one paired net rig operated on Saturdays and the other operated on Sundays. A pulley system was used to raise and lower the nets and safely retrieve birds from the upper net panels. Trammel spacing was standardized at 0.56 m such that the ground-level net spanned 0.50–2.74 m above the ground and the elevated net spanned 2.74–4.98 m above the ground. An additional paired net rig was operated 1993–1998 on multiple days each week, after which its use was discontinued. All nets were 12 m x 2.6 m made of polyester with 4 tiers and 30 mm mesh. Net sites were titled by their distance in meters upstream along Coyote Creek from the San Francisco Bay. The two

regularly operated paired net sites were titled 9280 and 9590, and the discontinued paired net site was titled 8735 (Table 1). All three paired net rigs were in the mature riparian corridor bordering the creek.

Nets were opened ~30 min before sunrise and closed after five hours. Effort was recorded for each day where 1 net hour represented one 12 m x 2.6 m net open for 1 hr. Nets were checked every 30 min. Birds were banded with USGS aluminum bands and we recorded the capture date, time, and net for each bird. Age and sex of birds were determined when possible following Pyle (1997), and standard body condition, plumage, and morphological data were collected before birds were released. Recaptured individuals were similarly processed. Hummingbirds were banded only from 1993 to 1999, so the analyses of hummingbirds includes only those years.

Analytical methods

Foraging guilds

Taxa were classified into the following height-based foraging guilds, similar to those used by DeGraaf and Wentworth (1986), based on a review of the “Diet and Foraging” sections of their Birds of the World accounts (Billerman et al. 2020): aerial (flycatchers), hovering (hummingbirds), ground (foragers on ground substrates), lower strata (foragers above the ground, in shrubs and subcanopy but below midcanopy), middle strata (foragers in tall shrubs and midcanopy), and upper strata (foragers in the canopy; see Table 2). Many species utilized multiple strata, in which cases all of those strata were included in that species’ classification; e.g., the Warbling Vireo *Vireo gilvus* “forages from just above ground to near top of canopy” (Gardali and Ballard 2020), so was classified as “lower to upper strata” (Table 2). We kept our classifications broad to avoid making overly specific determinations where significant variability may exist, or detailed data is lacking. When possible, we used foraging information specific to coastal California populations to make these classifications.

Minimum sample size determination

Bayesian analysis is well-suited to analyzing small sample sizes (Hox et al. 2012). However, determining the desired minimum sample size for Bayesian analyses is an area of ongoing research (Joseph and Bélisle 2019). For our analyses we aimed to balance conservatism with the value of utilizing data when possible. We targeted a credible interval length of ≤ 0.50 , because that was the

Table 2. Sample sizes of the study taxa from 1993 to 2020 captured in paired of ground-level and elevated nets at the Coyote Creek Field Station, Milpitas, CA, USA. Sample sizes represent the number of unique individual captures, which includes both newly banded birds and recaptures originally captured in any non-paired net. Four letter species codes that are used in our figures are provided. Foraging guild classifications are based on a review of each taxon's Birds of the World account (see Methods). E = biased toward capture in elevated nets; G = biased toward capture in ground-level nets. Bias is given only for taxa with a significant bias detected.

Taxon	Code	Foraging Guild	Sample Sizes		Probability of Ground-level Capture Mean (95% CI)	Bias
			Ground-level	Elevated		
Mourning Dove <i>Zenaida macroura</i>	MODO	Ground	8	18	0.321 (0.167–0.498)	E
Black-chinned Hummingbird <i>Archilochus alexandri</i>	BCHU	Hovering	6	19	0.258 (0.115–0.432)	E
Anna's Hummingbird <i>Calypte anna</i>	ANHU	Hovering	45	83	0.355 (0.276–0.440)	E
Allen's Hummingbird <i>Selasphorus sasin</i>	ALHU	Hovering	7	9	0.443 (0.231–0.671)	
Rufous Hummingbird <i>Selasphorus rufus</i>	RUHU	Hovering	13	30	0.310 (0.190–0.449)	E
Downy Woodpecker <i>Dryobates pubescens</i>	DOWO	Lower to Upper Strata	21	36	0.373 (0.258–0.496)	E
Nuttall's Woodpecker <i>Dryobates nuttallii</i>	NUWO	Lower to Upper Strata	12	14	0.465 (0.287–0.647)	
Northern Flicker <i>Colaptes auratus</i>	NOFL	Ground	6	9	0.408 (0.353–0.466)	
Willow Flycatcher <i>Empidonax traillii</i>	WIFL	Aerial	2	12	0.190 (0.044–0.411)	E
Western Flycatcher <i>Empidonax difficilis/occidentalis</i>	WEFL	Aerial	353	408	0.464 (0.429–0.500)	E
Black Phoebe <i>Sayornis nigricans</i>	BLPH	Aerial	50	50	0.500 (0.405–0.597)	
Warbling Vireo <i>Vireo gilvus</i>	WAVI	Lower to Upper Strata	10	20	0.342 (0.190–0.514)	
California Scrub-Jay <i>Aphelocoma californica</i>	CASJ	Ground to Lower Strata	9	7	0.554 (0.327–0.768)	
Chestnut-backed Chickadee <i>Poecile rufescens</i>	CBCH	Middle to Upper Strata	102	186	0.355 (0.300–0.410)	E
Bushtit <i>Psaltiriparus minimus</i>	BUSH	Lower to Upper Strata	105	112	0.483 (0.417–0.552)	
Golden-crowned Kinglet <i>Regulus satrapa</i>	GCKI	Lower to Upper Strata	13	26	0.341 (0.207–0.495)	E
Ruby-crowned Kinglet <i>Regulus calendula</i>	RCKI	Lower to Upper Strata	120	147	0.450 (0.390–0.509)	
Pacific Wren <i>Troglodytes pacificus</i>	PAWR	Ground to Lower Strata	9	3	0.713 (0.460–0.906)	
Bewick's Wren <i>Thryomanes bewickii</i>	BEWR	Ground to Lower Strata	57	28	0.666 (0.562–0.761)	G
Northern Mockingbird <i>Mimus polyglottos</i>	NOMO	Ground to Lower Strata	6	6	0.499 (0.254–0.741)	
Varied Thrush <i>Ixoreus naevius</i>	VATH	Ground	7	9	0.443 (0.234–0.671)	
Swainson's Thrush <i>Catharus ustulatus</i>	SWTH	Ground to Lower Strata	255	112	0.694 (0.645–0.739)	G
Hermit Thrush <i>Catharus guttatus</i>	HETH	Ground to Lower Strata	339	175	0.658 (0.616–0.698)	G
American Robin <i>Turdus migratorius</i>	AMRO	Ground	42	35	0.543 (0.430–0.652)	
House Finch <i>Haemorhous mexicanus</i>	HOFI	Ground	52	68	0.435 (0.347–0.524)	
American Goldfinch <i>Spinus tristis</i>	AMGO	Ground	14	64	0.187 (0.109–0.280)	E
Fox Sparrow <i>Passerella iliaca</i>	FOSP	Ground	96	36	0.724 (0.648–0.798)	G
Gambel's White-crowned Sparrow <i>Zonotrichia leucophrys gambelii</i>	GWCS	Ground	15	18	0.462 (0.299–0.617)	
Puget-sound White-crowned Sparrow <i>Zonotrichia leucophrys pugetensis</i>	PSWS	Ground	56	44	0.559 (0.461–0.657)	
Golden-crowned Sparrow <i>Zonotrichia atricapilla</i>	GCSP	Ground	100	71	0.585 (0.510–0.655)	G
Song Sparrow <i>Melospiza melodia</i>	SOSP	Ground	216	96	0.691 (0.639–0.740)	G
Lincoln's Sparrow <i>Melospiza lincolni</i>	LISP	Ground to Lower Strata	31	18	0.630 (0.494–0.757)	
California Towhee <i>Melospiza crissalis</i>	CALT	Ground	37	36	0.505 (0.393–0.615)	
Bullock's Oriole <i>Icterus bullockii</i>	BUOR	Lower to Upper Strata	42	53	0.444 (0.345–0.544)	
Brown-headed Cowbird <i>Molothrus ater</i>	BHCO	Ground	7	5	0.573 (0.315–0.799)	
Orange-crowned Warbler <i>Leiothlypis celata</i>	OCWA	Lower to Upper Strata	65	78	0.456 (0.376–0.534)	
Common Yellowthroat <i>Geothlypis trichas</i>	COYE	Ground to Lower Strata	83	49	0.627 (0.544–0.706)	G
Yellow Warbler <i>Setophaga petechia</i>	YEWA	Lower to Upper Strata	30	54	0.361 (0.265–0.467)	E
Audubon's Yellow-rumped Warbler <i>Setophaga coronata auduboni</i>	AUWA	Middle to Upper Strata	172	399	0.302 (0.264–0.340)	E
Myrtle Yellow-rumped Warbler <i>Setophaga coronata coronata</i>	MYWA	Middle to Upper Strata	111	161	0.408 (0.353–0.466)	E
Townsend's Warbler <i>Setophaga townsendi</i>	TOWA	Lower to Upper Strata	5	10	0.355 (0.154–0.588)	
Wilson's Warbler <i>Cardellina pusilla</i>	WIWA	Lower to Upper Strata	117	137	0.461 (0.402–0.522)	
Black-headed Grosbeak <i>Pheucticus melanocephalus</i>	BHGR	Lower to Upper Strata	13	15	0.466 (0.294–0.648)	
Totals			2865	2970		

maximum interval length for which it would be possible to detect a height bias. For single proportion binomial models, we used a minimum sample size of 12, which was determined by examining the minimum sample size calculated using the three main approaches to Bayesian binomial sample size determination (average coverage criterion, average length criterion, and worst outcome criterion), with $\alpha = 0.05$ and maximum credible interval length of 0.50, and then selecting the largest of those three calculated sample sizes (Joseph et al. 1995). For difference between two proportions binomial models, we used a minimum

sample size of 28 for each group, which was similarly determined by calculating the minimum sample size using the three methods named above and with the same alpha and credible interval settings, and then choosing the largest of the three calculated sample sizes. In both cases, the largest sample sizes proved to be those calculated using the worst outcome criterion, which is generally found to be the most conservative (Joseph et al. 1995). There is no established method for calculating the minimum sample size for a Bayesian fixed effects analysis, so for the analysis of net location we used the minimum sample size for single

proportion binomial models for each net location, i.e., each analyzed net location had a minimum sample size of 12. We additionally required a total minimum sample size of $(12n \times 1.25)$, where n was the number of net locations analyzed, resulting in total minimum sample sizes of either 30 or 45, depending on whether the analysis included two or all three net locations.

Statistical modeling

We filtered our data to include the first capture of each individual at any of the three paired net rigs. This included newly banded birds as well as recaptures that were originally captured at non-paired (ground-level-only) net locations, which we refer to as “new recaptures.” We treated height of capture net (ground-level or elevated) at the paired net rig as a Bernoulli random variable. Single proportion binomial models were used to estimate the probability of ground-level capture for taxa that met the sample size criterion of $n \geq 12$, where n = number of first captures. We added fixed effects for each net location (8735, 9280, and 9590) for all taxa with sufficient captures to assess whether capture height biases varied between locations. Difference between two proportions binomial models were used to estimate differences by capture history (newly banded or new recapture), age, sex, and season for all taxa that met the sample size criterion for each group of size $n \geq 28$. To assess differences between sexes, only data from known-sex individuals, as determined by reliable plumage characters and/or breeding physiology, were included. Our assessment of age differences focused on captures from June through December where individuals of most taxa could reliably be separated into hatch year (HY) and after-hatch year (AHY) age classes. To examine seasonal patterns, captures were partitioned among winter (December–February), spring (March–May), summer (June–August), and fall (September–November).

All models, except for that concerning the feeding guilds, were built in a Bayesian framework using the BUGS language (Lunn et al. 2000). We estimated each parameter’s posterior distribution with three parallel Markov Chain Monte Carlo (MCMC) chains using Gibbs sampling in JAGS v. 4.3.0 (Plummer 2017) called from the package ‘jagsUI’ (Kellner 2019) in R v. 3.4.2 (R Core Team 2017). For the single and difference between two proportion binomial models, uninformative priors of the form were used. For binomial models assessing the fixed effects of each net location, uninformative priors with a normal distribution with a mean of 0 and variance of 1000 were used for the intercepts and slopes. Inspection of the trace plots and Gelman-Rubin diagnostic confirmed successful convergence of parameters (Gelman et al. 2004). For single proportion models, we considered results significant if the 95% credible interval did not overlap with 0.5. For the difference of two proportions models we considered results significant if the 95% credible intervals did not overlap with 0.

To test whether observed capture height biases were related to foraging guilds, we ran a generalized linear model of the proportion of captures that were in the elevated net for each species, weighted by the total number of captures for each species, with foraging guild as a fixed effect, and with a binomial distribution and a logit link.

We did not correct for multiplicities among our tests. Multiplicity corrections in Bayesian statistics is a growing field with no consensus on the appropriate analytical techniques (Westfall et al. 1997, Berry and Hochberg 1999, Sjölander and Vansteelandt 2019). Some have argued that such corrections are not necessary for many Bayesian applications (Gelman et al. 2012, Sjölander and Vansteelandt 2019).

RESULTS

From 1993 to 2020, operation of the three paired net rigs resulted in 7312 captures of 81 taxa. At all three rigs, the elevated net captured slightly more birds than the corresponding ground-level net, but these differences were not significant (Table 1). Forty-three taxa met the sample size criteria for our single species models (Table 2). Capture height biases were detected in 20 of these taxa (Fig. 1), with seven more likely to be captured in ground-level nets and 13 more likely to be captured in elevated nets. The taxa with ground-level biases included two thrushes and three sparrows, while those with elevated net biases included three hummingbirds and two flycatchers. Interestingly, while both Yellow-rumped Warbler subspecies analyzed were biased toward the elevated nets, their 95% credible intervals for the probability of ground-level capture did not overlap. Audubon’s Yellow-rumped Warblers *Setophaga coronata auduboni* were more likely to be captured in the elevated nets than Myrtle Yellow-rumped Warblers *S. c. coronata*.

Net location effects

Of the 43 taxa analyzed for overall capture height biases, there were sufficient sample sizes to evaluate location effects at all three net locations (8735, 9280, and 9590) for 16 taxa and at the two regularly operated net locations (9280 and 9590) for an additional 12 taxa (Fig. 2, see Table A1.1 for sample sizes). There were no instances of taxa having opposite biases at different net locations. Of the 20 taxa with overall capture height biases, four (Mourning Doves *Zenaidura macroura*, Black-chinned Hummingbirds *Archilochus alexandri*, Rufous Hummingbirds *Selasphorus rufus*, and Willow Flycatchers *Empidonax traillii*) did not have sufficient sample sizes to evaluate net location effects. Eight of the 16 taxa with overall capture height biases and sufficient sample size (Anna’s Hummingbirds *Calypte anna*, Bewick’s Wrens *Thryomanes bewickii*, Swainson’s Thrush *Catharus ustulatus*, Hermit Thrush *Catharus guttatus*, American Goldfinches *Spinus tristis*, Fox Sparrows *Passerella iliaca*, Song Sparrows *Melospiza melodia*, and Audubon’s Yellow-rumped Warblers) exhibited consistent biases at all net locations evaluated. For the other eight taxa with overall capture height biases and sufficient sample size (Downy Woodpeckers *Dryobates pubescens*, Western Flycatchers *Empidonax difficilis/occidentalis*, Chestnut-backed Chickadees *Poecile rufescens*, Golden-crowned Kinglets *Regulus calendula*, Golden-crowned Sparrows *Zonotrichia atricapilla*, Common Yellowthroats *Geothlypis trichas*, Yellow Warblers *Setophaga petechia*, and Myrtle Yellow-rumped Warblers), significant effects at 1–2 net locations drove the overall effect. Additionally, there were four taxa (Bushtits *Psaltiriparus minimus*, Ruby-crowned Kinglets *Regulus satrapa*, Orange-crowned Warblers *Leiothlypis celata*, and Wilson’s Warblers *Cardellina pusilla*) that did not have overall capture height biases but had at least one net location with a significant effect on capture height bias.

Fig. 1. Probabilities of ground-level capture estimated for 43 taxa from paired ground-level and elevated mist-net capture data 1993–2020 at the Coyote Creek Field Station, Milpitas, CA, USA. The black bars represent the upper and lower bounds of the 95% credible intervals. The boxes around each taxa code are for ease of reading and are centered on each mean. Taxa with their entire interval < 0.5 were biased toward elevated nets while taxa with their entire interval > 0.5 were biased toward ground-level nets. Four-letter codes are given in Table 2.

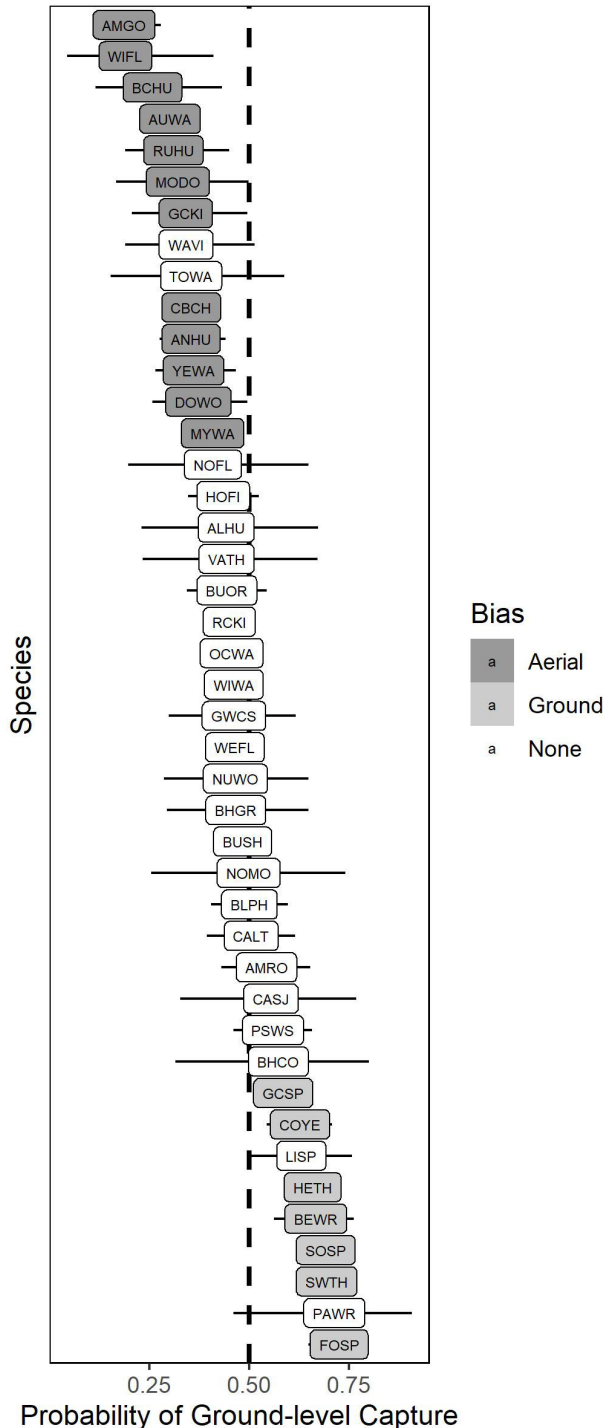
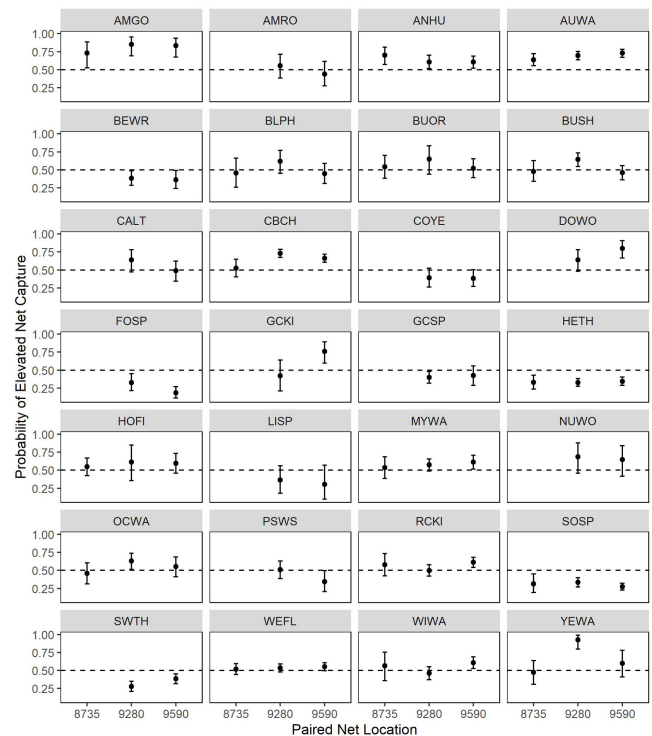


Fig. 2. Probabilities of elevated net capture estimated for 16 taxa at all three net locations and 12 taxa at the two regularly operated net locations from 1993 to 2020 at the Coyote Creek Field Station, Milpitas, CA, USA. Black dots represent the mean and black bars represent the upper and lower bounds of the 95% credible intervals. Taxa with their entire interval < 0.5 were biased toward the elevated net, while taxa with their entire interval > 0.5 were biased toward the ground-level net. Four-letter codes are given in Table 2.



Capture history effects

We assessed differences in the probability of ground-level capture between newly banded and newly recaptured birds for 15 taxa (see Table A1.2 for summary statistics and Table A1.3 for sample sizes). We found significant differences for only the Myrtle Yellow-rumped Warblers, which had a higher probability of ground-level capture for newly banded birds than for newly recaptured birds. Both the newly banded and newly recaptured Myrtle Yellow-rumped Warblers were biased toward elevated nets, but the bias was significantly greater for recaptured birds.

Demographic differences

Of five taxa with sufficient known age captures in the summer and fall (see Table A1.4 for summary statistics and Table A1.5 for sample sizes), only Swainson's Thrush showed an age-related capture height bias: AHY birds were more likely to be captured in ground-level nets than HY birds. Of 11 taxa with sufficient known sex captures (see Table A1.6 for summary statistics and Table A1.7 for sample sizes), only Anna's Hummingbirds showed a sex-related capture height bias, with females more likely to be captured in ground-level nets than males.

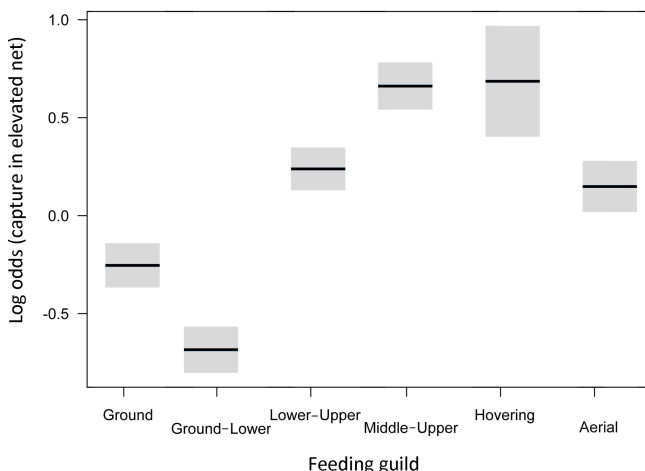
Table 3. Capture height biases detected among 43 taxa at the Coyote Creek Field Station, Milpitas, CA, USA, from 1993 to 2020 broadly aligned with foraging guild classifications. Analysis with a generalized linear model with a binomial distribution supported this relationship. The lower to upper guild was the reference level for comparison and so lacks statistics and has NAs.

Foraging guild	Number of Taxa with Ground bias (%)	Number of Taxa with Elevated bias (%)	Taxa	Estimate±SE	z	P
Aerial	0 (0)	2 (67)	3	-0.090±0.088	-1.01	0.311
Hovering	0 (0)	3 (75)	4	0.447±0.156	2.86	0.004
Middle to upper	0 (0)	3 (100)	3	0.423±0.085	4.99	<0.001
Lower to upper	0 (0)	3 (25)	12	NA	NA	NA
Ground to lower	4 (50)	0 (0)	8	-0.923±0.084	-11.02	<0.001
Ground	3 (23)	2 (15)	13	-0.492±0.082	-6.00	<0.001

Foraging guild patterns

Capture height biases differed significantly among foraging guilds and broadly followed the expected height patterns (Fig. 3, Table 3). Ground-level biases were detected only in taxa belonging to the ground and ground to lower foraging guilds. Biases toward capture in elevated nets were detected in most taxa belonging to the aerial, hovering, and middle to upper foraging guilds, and zero taxa belonging to the ground to lower foraging guild. However, contrary to expectation, biases toward capture in elevated nets were also detected in two taxa belonging to the ground foraging guild (American Goldfinches and Mourning Doves). The ground and ground to lower guilds were less likely to be captured in elevated nets than the lower to upper guild, and the middle to upper and hovering guilds were more likely to be captured in elevated nets than the lower to upper guild. The aerial guild did not differ from the lower to upper guild.

Fig. 3. Estimates of the probability of capture in elevated nets shown as the logarithm of the odds ratio for the foraging guilds analyzed in this study among 43 taxa captured from 1993 to 2020 at the Coyote Creek Field Station, Milpitas, CA, USA. Black lines represent the estimates (across-species means weighted by sample size) from the generalized linear model and the gray shaded areas represent the 95% confidence intervals.



Seasonal differences

We assessed seasonal differences for 18 taxa that met the sample size criteria for at least two seasons (see Table A1.8 for summary

statistics and Table A1.9 for sample sizes). Only seasons for which there was sufficient sample size were assessed. We found significant differences for five taxa: (1) Anna's Hummingbirds were more likely to be captured in ground-level nets in the winter compared the fall; (2) Ruby-crowned Kinglets were more likely to be captured in ground-level nets in the winter compared to the spring; (3) Swainson's Thrush were more likely to be captured in ground-level nets in the spring compared to the fall; and both (4) Song Sparrows and (5) Common Yellowthroats were more likely to be captured in ground-level nets in the spring compared to the summer.

DISCUSSION

Almost half the taxa in this study (46.5%) exhibited capture height biases, with 13 taxa biased toward capture in elevated nets and seven taxa biased toward ground-level nets. We found evidence that foraging height impacted capture height bias, and that biases differed among seasons. There was less support for differences in capture height bias by net location, capture history, age, or sex, although a few taxa did exhibit these effects. Together, these results suggest that using only ground-level mist-nets has greater potential to introduce bias than previously thought.

Although other investigators have grouped species in feeding guilds when analyzing methodological biases (see Vecchi and Alves 2015 on capture height, Gilbert et al. 2021 on visibility bias in waterbird surveys, and Vold et al. 2017 on comparisons between visual and acoustic surveys), to our knowledge this is the first study that has tested for capture biases based on foraging height guilds. As expected, the probability of capturing individuals of each guild in ground-level nets broadly reflected the guilds' vertical foraging strata. The middle to upper and hovering guilds were significantly more biased toward elevated capture than the lower to upper guild, which in turn was significantly more biased toward elevated capture than the ground to lower and ground guilds. The aerial guild was not different from the ground to upper guild, which may be related to the fact that its component species—all flycatchers—often forage from low perches (Billerman et al. 2020). Unexpectedly, two ground foraging taxa, Mourning Doves and American Goldfinches, had biases toward capture by elevated nets. This discrepancy highlights the limitations of attributing capture height biases to foraging habits alone: foraging is only one of many circumstances that may lead to capture in a mist net (Bonter et al. 2008, LaBarbera and Scullen 2021). Nevertheless, we found that foraging guilds do reflect the general patterns of capture height biases, suggesting that foraging guild classification

could be a good approximation for the height at which a taxon most often encounters a mist net. Researchers may be able to use known foraging height as a predictor of overall capture height bias, which could be valuable when designing mist-net sampling schemes.

Comparison of our species-level results to those of Bonter et al. (2008) shows greater consistency in ground-level biases than biases toward elevated nets. Of 14 species analyzed in both papers, we detected opposite biases for only two: Willow Flycatchers (analyzed by Bonter et al. 2008 as Traill's Flycatcher *Empidonax alnorum/traillii*, which may also include Alder Flycatchers, a sister species difficult to distinguish from Willow Flycatcher in the hand and that share similar habitat preferences and life histories) and Yellow Warblers were biased toward elevated nets in our study but ground-level nets in Bonter et al. (2008). We detected the same ground-level biases for four taxa (Swainson's Thrush, Hermit Thrush, Common Yellowthroats, and Song Sparrows). None of the five taxa identified in our study as having biases toward elevated nets that were also analyzed by Bonter et al. (2008) had such a bias in that paper. Unfortunately, none of the taxa with elevated biases in Bonter et al. (2008) were analyzed in our study. Although limited by small sample size, these comparisons suggest biases toward elevated net capture may be more variable than those for the ground-level, at least between these two study sites. This may reflect habitat structure: in temperate woodland, the height of the ground and ground-level features (such as herbaceous vegetation) are probably more consistent than overstory vegetation structure. Bonter et al. (2008) report that the top of their elevated net rigs extended above the canopy at their site, whereas the canopy at our study site extended above the tops of our elevated net rigs by ~4 m. Bonter et al. (2008) speculate that the resulting increased sun and wind exposure of their elevated nets, in comparison to their ground-level nets, contributed to increased net avoidance behavior at the elevated net level. In contrast, our elevated nets remained under the protection of the canopy vegetation. The data are consistent with this proposed effect of relative canopy height: although the captures in Bonter et al. (2008) were substantially biased toward the ground-level nets, we did not find a difference in overall captures between our two net heights. Comparison between only two studies is inherently limited, however. The variation between these studies highlights the need for wider usage and analysis of paired net rigs in different habitats.

Capture biases were largely consistent among our three net locations: of 28 taxa, none exhibited opposing capture height biases across locations. We know of only one other study that looked for differences in capture height biases between net locations (Fitzgerald et al. 1989), which similarly found that most species showed consistent patterns between net sites within the same habitat. This consistency is to be expected of nets located in the same habitat with the same bird community if capture height bias is driven by factors such as habitat and taxon. This low net-to-net variation also suggests that researchers may be able to quantify capture height bias with a small number of nets and safely generalize from those. In our analyses, four taxa did not exhibit biases overall, but did at specific net-pairs: Bushtits, Ruby-crowned Kinglets, Orange-crowned Warblers, and Wilson's Warblers. This may be due to very small-scale geographic variation, such as specific habitat features or differences in

perceived predation risk that alter the height at which these birds fly (Cimprich et al. 2005). Alternatively, the net-to-net variation could be due to varying sample sizes at different nets resulting in some net locations having less power to detect small biases than others. Future work could place paired net rigs within multiple habitat types and test whether habitat features such as canopy height or understory height impact net-to-net variation in capture height biases.

We found little support for an effect on capture height bias of individual capture history, i.e., whether the bird had been previously caught (in a standard ground-level net, not a paired net rig): of 14 taxa, only one (7.1%) had a significant difference. This differs from Fitzgerald et al.'s (1989) observation of capture history-based height differences in more than one-quarter of their focal species. Our low rate of observed differences based on capture history suggests that there is a low risk of capture history confounding capture height bias analyses, and vice versa. We found that in Myrtle Yellow-rumped Warblers, newly banded birds were more likely to be captured in ground-level nets than recaptures. Possible explanations for this apparent upward movement of recaptured vs. newly-captured birds include (1) a net avoidance behavior (Marques et al. 2013, Roche et al. 2013) where birds previously captured at the ground level alter their activity patterns to higher habitat strata, and/or (2) a transient effect (Fitzgerald et al. 1989) where transient individuals, which are over-represented among newly banded birds (Nur et al. 2004), may move through the habitat at a lower height than resident or overwintering individuals, which are over-represented among recaptures. Net avoidance and cryptic differences between transient and (relatively) resident individuals represent important challenges in analyzing bird banding data (MacArthur and MacArthur 1974, Remsen and Good 1996, Nur et al. 2004, Roche et al. 2013), particularly when modeling survival. Although our focal taxa showed little association between capture history and capture height bias, Fitzgerald et al.'s (1989) analysis suggests that such associations can occur with moderate frequency. For taxa in which they do occur, the selection of net height could be a useful tool for researchers wishing to focus primarily on either resident or transient individuals. For example, our results suggest that a project interested in resident (over-wintering) Myrtle Yellow-rumped Warblers would be well-served by prioritizing elevated over ground-level nets.

Capture height biases at the taxon level may not be problematic for data analyses so long as the sample of the population at the ground-level remains representative of the total population available for capture. Capture height biases are more troubling if they covary with some variable of interest. Remsen and Good (1996) speculated that ground-level nets may bias samples in demographic studies if species differ in vertical habitat use by age or sex. With respect to age and sex, which we were able to analyze for 5 and 11 taxa, respectively, we found only one instance for each variable where the use of only ground-level nets would impact capture data: female Anna's Hummingbirds and after-hatch-year Swainson's Thrush were more likely to be captured at the ground-level than their male or hatch-year counterparts, respectively. For Anna's Hummingbirds, this difference may be explained by the males' aerial display, which involves the bird rising up to 35 m above the ground and then plunging in a rapid dive (Clark and Russell 2020). It is unknown why after-hatch-year

Swainson's Thrush were captured at lower heights than hatch-years, but after-hatch-year Swainson's Thrush possess substantially higher fat stores during fall migration than hatch-years (Woodrey and Moore 1997), suggesting age differences in foraging strategy or efficiency. Broadly, our results suggest demographic differences in capture height biases are uncommon, as for both age and sex they were present in < 20% of taxa analyzed in this study. This is consistent with Bonter et al.'s (2008) migration season findings, although they too were only able to analyze age in < 10 taxa and sex in < 15 taxa. They speculated that sex might impact capture height bias more commonly during the breeding season, but seven of our eleven analyzed taxa breed at CCFS, and only one showed an effect of sex. More data on a broader variety of taxa and from more geographic regions are needed before the potential confounding impacts of demographic differences in capture height bias can be reasonably disregarded.

Seasonal changes in vertical habitat use may also bias captures and could be of particular concern at migration monitoring stations (Hutto 1985, Fitzgerald et al. 1989, Bonter et al. 2008). Of 15 taxa analyzed, 5 showed significant seasonal effects on capture height, including residents (Anna's Hummingbirds and Song Sparrows), short-distance migrants (Ruby-crowned Kinglets and Common Yellowthroats), and a long-distance migrant (Swainson's Thrush). Swainson's Thrush had a greater ground-level bias in the spring than in the fall, which is consistent with capture height bias shifts between spring and fall migration observed in four other species (Bonter et al. 2008). Bonter et al. (2008) suggest that this may be due to reduced vegetative cover at higher strata in the spring compared to the fall. Song Sparrows, which are resident at our study site year-round, were captured higher in the summer than they were in the spring or the fall. Common Yellowthroats, which primarily breed at our study site (though some individuals overwinter), were also captured higher in the summer than in the spring. Ruby-crowned Kinglets, which overwinter at our study site, were captured higher in the spring than the winter, in contrast to the opposite shift observed in two New Zealand species by Fitzgerald et al. (1989). Seasonal shifts may reflect changes in food resources, usage of higher strata by dispersing birds, or differences in habitat use related to breeding (Hutto 1985, Streby et al. 2014). Seasonal changes in capture height bias are likely to be habitat-specific, because they are likely impacted by habitat structure, food resources, and interspecies interactions (Hutto 1985, Bonter et al. 2008); therefore, researchers should use caution when extrapolating results from one study area to another.

Capture height biases at our study site were common and varied among taxa, feeding guilds, and seasons. These biases were largely not affected by net location, capture history, or demography, although there were exceptions. Further research should test for capture height biases in other taxa and geographic locations, investigate the mechanisms that produce variation in capture height biases, and further consider how to improve mist-netting methods to avoid any confounding impacts of these patterns. We urge the avian monitoring community to consider issues of capture height and, where possible, deploy mist-nets in a manner that allows such effects to be detected. For example, as a result of this study Coyote Creek Field Station has constructed additional paired net rigs in different habitat types and started recording the height of the net panel in which each bird is captured. Mist-netting

is one of the most important methods for avian research (Saracco et al. 2008), and therefore investment in validating and improving mist-netting protocols will improve the data underlying widespread efforts toward research and conservation.

Responses to this article can be read online at:

<https://journal.afonet.org/issues/responses.php/21>

Author Contributions:

The authors DJT and KL were sub-permitted banders for the Coyote Creek Field Station. DJT developed the idea for this study and collaborated with KL to build research questions and design analyses. DJT analyzed the data. Both authors wrote, edited, and gave final approval for the manuscript.

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Josh Scullen and Dan Wenny gave important feedback throughout the development of this study. Dozens of volunteers contributed to data collection. Michelle Stantial assisted with model-building. No funders had input into the content of the manuscript. CCFS protocols follow the Guidelines to the Use of Wild Birds in Research (Fair et al. 2010) as well as best practices established by the North American Banding Council. Banding is authorized under federal permit #22109.

Data Availability:

All bird banding data from under our Federal permit #22109 is publicly available by request from the USGS. Upon publication we will make our code and models available on the Dryad archiving service.

LITERATURE CITED

- Bart, J., C. Kepler, P. Sykes and C. Bocetti. 1999. Evaluation of mist-net sampling as an index to productivity in Kirtland's Warblers. *Auk* 116:1147-1151. <https://doi.org/10.2307/4089698>
- Berry, D. A., and Y. Hochberg. 1999. Bayesian perspectives on multiple comparisons. *Journal of Statistical Planning and Inference* 82:215-227. [https://doi.org/10.1016/S0378-3758\(99\)00044-0](https://doi.org/10.1016/S0378-3758(99)00044-0)
- Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg, editors. 2020. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow>
- Biro, P. A., and N. J. Dingemanse. 2009. Sampling bias resulting from animal personality. *Trends in Ecology & Evolution* 24:66-67. <https://doi.org/10.1016/j.tree.2008.11.001>
- Bonter, D. N., E. W. Brooks, and T. M. Donovan. 2008. What are we missing with only ground-level mist-nets? Using elevated nets at a migration stopover site. *Journal of Field Ornithology* 79:314-320. <https://doi.org/10.1111/j.1557-9263.2008.00179.x>
- Cimprich, D. A., M. S. Woodrey, and F. R. Moore. 2005. Passerine migrants respond to variation in predation risk during stopover.

- Animal Behaviour 69:1173-1179. <https://doi.org/10.1016/j.anbehav.2004.07.021>
- Clark, C. J., and S. M. Russel. 2020. Anna's Hummingbird (*Calypte anna*), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.annhum.01>
- DeGraaf, R. M., and J. M. Wentworth. 1986. Avian guild structure and habitat associations in suburban bird communities. Urban Ecology 9:399-412. [https://doi.org/10.1016/0304-4009\(86\)90012-4](https://doi.org/10.1016/0304-4009(86)90012-4)
- Derlindati, E. J., and S. M. Caziani. 2005. Using canopy and understory mist-nets and point counts to study bird assemblages in Chaco forests. Wilson Bulletin 117:92-99. <https://doi.org/10.1676/03-063>
- DeSante, D. F., K. M. Burton, P. Velez, D. Froehlich, D. Kaschube, and S. Albert. 2020. MAPS manual: 2020 protocol. Instructions for the establishment and operation of constant-effort bird-banding stations as part of the monitoring avian productivity and survivorship program. The Institute for Bird Populations, Petaluma, California, USA.
- DeSante, D. F., and D. R. Kaschube. 2009. The monitoring avian productivity and survivorship (MAPS) program 2004, 2005, and 2016 report. Bird Populations 9:86-269.
- DeSante, D. F., D. R. O'Grady, and P. Pyle. 1999. Measures of productivity and survival derived from standardized mist-netting are consistent with observed population changes. Bird Study 46:178-188. <https://doi.org/10.1080/00063659909477244>
- Domènech, J., and J. C. Senar. 1997. Trapping methods can bias age ratio in samples of passerine populations. Bird Study 44:348-354. <https://doi.org/10.1080/00063659709461070>
- Dufour, K. W., and P. J. Weatherhead. 1991. A test of the condition-bias hypothesis using Brown-headed Cowbirds trapped during the breeding season. Canadian Journal of Zoology 69:2686-2692. <https://doi.org/10.1139/z91-377>
- Dunn, E. H., and C. J. Ralph. 2004. The use of mist-nets as a tool for bird population monitoring. Studies in Avian Biology 29:1-6.
- Fair, J., E. Paul, and J. Jones, editors. 2010. Guidelines to the use of wild birds in research. Ornithological Council, Washington, D.C., USA.
- Fitzgerald, B. M., H. A. Robertson, and A. H. Whitaker. 1989. Vertical distribution of birds mist-netted in a mixed lowland forest in New Zealand. Notornis 36:311-321.
- Gardali, T. and G. Ballard. 2020. Warbling Vireo (*Vireo gilvus*), version 1.0. In A. F. Poole and F. B. Gill, editors. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.warvir.01>
- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Second edition. Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Gelman, A., J. Hill, and M. Yajima. 2012. Why we (usually) don't have to worry about multiple comparisons. Journal of Research on Educational Effectiveness 5:189-211. <https://doi.org/10.1080/19345747.2011.618213>
- Gilbert, A. D., C. N. Jacques, J. D. Lancaster, A. P. Yetter, and H. M. Hagy. 2021. Visibility bias of waterbirds during aerial surveys in the nonbreeding season. Wildlife Society Bulletin 45:6-15. <https://doi.org/10.1002/wsb.1150>
- Hox, J., R. van de Schoot, and S. Matthijsse. 2012. How few countries will do? Comparative survey analysis from a Bayesian perspective. Survey Research Methods 6:87-93. <https://doi.org/10.18148/srm/2012.v6i2.5033>
- Hutto, R. L. 1985. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: competition mediated? Auk 102:12-132. <https://doi.org/10.2307/4086827>
- Insley, H., and B. Etheridge. 1997. Catching bias in cannon and mist netted samples of Redshanks *Tringa totanus* on the Inner Moray Firth. Ringing & Migration 18:70-77. <https://doi.org/10.1080/03078698.1997.9674144>
- Joseph, L., and P. Bêlisle. 2019. Bayesian consensus-based sample size criteria for binomial proportions. Statistics in Medicine 38:4566-4573. <https://doi.org/10.1002/sim.8316>
- Joseph, L., D. B. Wolfson, and R. Du Berger. 1995. Sample size calculations for binomial proportions via highest posterior density intervals. Statistician 44:143-154. <https://doi.org/10.2307/2348439>
- Karr, J. R. 1981. Surveying birds with mist-nets. Studies in Avian Biology 6:62-67.
- Kellner, K. 2019. jagsUI: A wrapper around "rjags" to streamline "JAGS" analyses.
- LaBarbera, K., and J. C. Scullen. 2021. Using individual capture data to reveal large-scale patterns of social association in birds. Journal of Ornithology 162:795-811. <https://doi.org/10.1007/s10336-021-01863-3>
- Larsen, R. J., K. A. Boegler, H. H. Genoways, W. P. Maselfield, R. A. Kirsch, and S. C. Pedersen. 2007. Mist netting bats, species accumulation curves, and the rediscovery of two bats on Montserrat (Lesser Antilles). Acta Chiropterologica 9:423-435. [https://doi.org/10.3161/1733-5329\(2007\)9\[423:MNBSAC\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[423:MNBSAC]2.0.CO;2)
- Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS - A Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10:325-337. <https://doi.org/10.1023/A:1008929526011>
- MacArthur, R. H., and A. T. MacArthur. 1974. On the use of mist nets for population studies of birds. Proceedings of the National Academy of Sciences 71:3230-3233. <https://doi.org/10.1073/pnas.71.8.3230>
- Marques, J. T., M. J. Ramos Pereira, T. A. Marques, C. D. Santos, J. Santana, P. Beja, and J. M. Palmeirim. 2013. Optimizing sampling design to deal with mist-net avoidance in Amazonian birds and bats. PLoS ONE 8(9):e74505. <https://doi.org/10.1371/journal.pone.0074505>
- Nur, N., G. R. Geupel and G. Ballard. 2004. Estimates of adult survival, capture probability, and recapture probability: evaluating and validating constant-effort mist-netting. Studies in Avian Biology 29:63-70.

- Pagen, R. W., F. R. Thompson III, and D. E. Burhans. 2002. A comparison of point-count and mist-net detections of songbirds by habitat and time-of-season. *Journal of Field Ornithology* 73:53–59. <https://doi.org/10.1648/0273-8570-73.1.53>
- Plummer, M. 2017. JAGS: Just Another Gibbs Sampler. [online] URL: <https://sourceforge.net/projects/mcmc-jags/>
- Pyle, P. 1997. Identification guide to North American birds Part I. Slate Creek, Bolinas, California, USA.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing Vienna, Austria.
- Remsen Jr., J. V., and D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. *Auk* 113:381–398. <https://doi.org/10.2307/4088905>
- Roche, E. A., C. R. Brown, M. B. Brown, and K. M. Lear. 2013. Recapture heterogeneity in Cliff Swallows: increased exposure to mist nets leads to net avoidance. *PLoS ONE* 8:e58092. <https://doi.org/10.1371/journal.pone.0058092>
- Saracco, J. F., D. F. Desante, and D. R. Kaschube. 2008. Assessing landbird monitoring programs and demographic causes of population trends. *Journal of Wildlife Management* 72:1665–1673. <https://doi.org/10.2193/2008-129>
- Silkey, M., N. Nur, and G. R. Geupel. 1999. The use of mist-net capture rates to monitor annual variation in abundance: a validation study. *Condor* 101:288–298. <https://doi.org/10.2307/1369992>
- Sjölander, A., and S. Vansteelandt. 2019. Frequentist versus Bayesian approaches to multiple testing. *European Journal of Epidemiology* 34:809–821. <https://doi.org/10.1007/s10654-019-00517-2>
- Spotswood, E. N., K. R. Goodman, J. Carlisle, R. L. Cormier, D. L. Humple, J. Rousseau, S. L. Guers, and G. G. Barton. 2012. How safe is mist netting? Evaluating the risk of injury and mortality to birds. *Methods in Ecology and Evolution* 3:29–38. <https://doi.org/10.1111/j.2041-210X.2011.00123.x>
- Stokes, A. E., B. B. Schultz, R. M. Degraaf, and C. R. Griffin. 2000. Setting mist nets from platforms in the forest canopy. *Journal of Field Ornithology* 71:57–65. <https://doi.org/10.1648/0273-8570-71.1.57>
- Streby, H. M., J. M. Refsnider, S. M. Peterson, and D. E. Anderson. 2014. Retirement investment theory explains patterns in songbird nest-site choice. *Proceedings of the Royal Society B: Biological Sciences* 281:20131834. <https://doi.org/10.1098/rspb.2013.1834>
- Vanderkist, B. A., X.-H. Xue, R. Griffiths, K. Martin, W. Beauchamp, and T. D. Williams. 1999. Evidence of male-bias in capture samples of Marbled Murrelets from genetic studies in British Columbia. *Condor* 101:398–402. <https://doi.org/10.2307/1370004>
- Vecchi, M. B., and M. A. S. Alves. 2015. Bird assemblage mist-netted in an Atlantic Forest area: a comparison between vertically-mobile and ground-level nets. *Brazilian Journal of Biology* 75:742–751. <https://doi.org/10.1590/1519-6984.00914>
- Vold, S. K., C. M. Handel, and L. B. McNew. 2017. Comparison of acoustic recorders and field observers for monitoring tundra bird communities. *Wildlife Society Bulletin* 41:566–576. <https://doi.org/10.1002/wsb.785>
- Wang, Y., and D. M. Finch. 2002. Consistency of mist-netting and point counts in assessing landbird species richness and relative abundance during migration. *Condor* 104:59–72. <https://doi.org/10.1093/condor/104.1.59>
- Westfall, P. H., W. O. Johnson, and J. M. Utts. 1997. A Bayesian perspective on the Bonferroni adjustment. *Biometrika* 84:419–427. <https://doi.org/10.1093/biomet/84.2.419>
- Woodrey, M. S., and F. R. Moore. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114:695–707. <https://doi.org/10.2307/4089289>

Appendix 1

Table A1.1. Sample sizes of the twenty-six taxa analyzed for the fixed effects of the three paired ground-level and elevated net locations (titled 8735, 9280, and 9590 based on the distance in meters upstream of the San Francisco Bay at our study site). All taxa with ≥ 28 captures from at least two of the paired net locations were included.

	8735		9280		9590	
	Ground- level	Elevated	Ground- level	Elevated	Ground- level	Elevated
Anna's Hummingbird	15	35	42	65	48	74
Downy Woodpecker			14	25	8	32
Western Flycatcher	80	86	144	166	137	169
Black Phoebe	12	10	13	21	26	21
Chestnut-backed Chickadee	30	33	61	165	87	171
Bushtit	23	21	38	69	55	47
Golden-crowned Kinglet			11	18	7	22
Ruby-crowned Kinglet	16	22	74	74	69	108
Bewick's Wren			53	33	37	21
Swainson's Thrush			112	43	108	67
Hermit Thrush	59	29	197	96	167	88
American Robin			15	19	18	14

House Finch	28	34	5	8	19	28
American Goldfinch	6	16	4	23	5	25
Fox Sparrow			39	19	75	17
Puget-sound White-crowned Sparrow			31	32	25	13
Golden-crowned Sparrow			84	56	30	22
Song Sparrow	35	16	150	75	252	95
Lincoln's Sparrow			14	8	9	4
California Towhee			13	23	25	24
Bullock's Oriole	17	20	7	13	24	26
Orange-crowned Warbler	25	21	25	43	21	26
Common Yellowthroat			33	21	41	25
Yellow Warbler	18	16	2	24	10	15
Audubon's Yellow-rumped Warbler	46	81	68	157	65	175
Myrtle Yellow-rumped Warbler	19	22	58	78	40	64
Wilson's Warbler	10	13	59	51	53	82

Table A1.2. Summary statistics for the posterior distributions of the difference between probabilities of ground-level capture for newly banded birds and new recaptures at the Coyote Creek Field Station, CA, from 1993-2020. A positive value indicates new birds were likely captured in the ground-level nets.

Taxa	Mean	SD	Credibility Interval	
			2.5%	97.5%
Chestnut-backed Chickadee	0.083	0.100	-0.120	0.271
Bushtit	0.056	0.070	-0.081	0.188
Ruby-crowned Kinglet	0.091	0.116	-0.139	0.312
Swainson's Thrush	0.056	0.075	-0.086	0.205
Hermit Thrush	-0.021	0.043	-0.104	0.060
Fox Sparrow	-0.028	0.076	-0.180	0.122
Puget-sound White-crowned Sparrow	0.068	0.098	-0.128	0.259
Golden-crowned Sparrow	0.035	0.076	-0.116	0.188
Song Sparrow	-0.117	0.062	-0.237	0.005
Orange-crowned Warbler	-0.018	0.088	-0.191	0.151
Common Yellowthroat	0.104	0.083	-0.060	0.263
Audubon's Yellow-rumped Warbler	-0.065	0.060	-0.179	0.055
Myrtle Yellow-rumped Warbler	0.147	0.070	0.001	0.277
Wilson's Warbler	0.066	0.095	-0.126	0.244

Table A1.3. Sample sizes of the fourteen taxa used in the newly banded and new capture analysis. All taxa with ≥ 28 captures of both newly banded individuals and new recaptures were included.

Taxa	Newly Banded		New Recapture	
	Ground	Elevated	Ground	Elevated
Chestnut-backed Chickadee	43	70	58	115
Bushtit	42	39	63	73
Ruby-crowned Kinglet	56	79	62	67
Swainson's Thrush	227	97	28	15
Hermit Thrush	213	114	125	61
Fox Sparrow	39	16	56	20
Puget-sound White-crowned Sparrow	27	18	28	25
Golden-crowned Sparrow	39	25	61	46
Song Sparrow	43	29	166	67
Orange-crowned Warbler	45	55	20	23
Common Yellowthroat	40	18	43	31
Audubon's Yellow-rumped Warbler	151	335	21	63
Myrtle Yellow-rumped Warbler	97	125	14	36
Wilson's Warbler	105	120	11	17

Table A1.4. Summary statistics for the posterior distributions of the difference between probabilities of ground-level capture for adult (AHY) and young (HY) individuals of five taxa banded at the Coyote Creek Field Station, CA, from 1993-2020. A positive value indicates a greater probability of ground-level capture for AHY birds.

Taxa	Mean	SD	Credibility Interval	
			2.5%	97.5%
Chestnut-backed Chickadee	-0.090	0.058	-0.203	0.026
Swainson's Thrush	0.178	0.069	0.044	0.312
Hermit Thrush	0.041	0.044	-0.043	0.126
Golden-crowned Sparrow	0.072	0.090	-0.103	0.246
Song Sparrow	0.039	0.059	-0.073	0.155

Table A1.5. Sample sizes of the five taxa used in the age-based analysis. All taxa with ≥ 28 captures of both adults (AHY) and young (HY) were included.

Taxa	HY		AHY	
	Ground	Elevated	Ground	Elevated
Chestnut-backed Chickadee	44	64	9	27
Swainson's Thrush	32	26	26	14
Hermit Thrush	145	79	53	31
Golden-crowned Sparrow	22	21	14	14
Song Sparrow	57	29	28	21

Table A1.6. Summary statistics for the posterior distributions of the difference between probabilities of ground-level capture for male and female individuals of eleven taxa banded at the Coyote Creek Field Station, CA, from 1993-2020. A negative value indicates a greater aerial height bias for males than females.

Taxa	Mean	SD	Credibility	
			Interval	
			2.5%	97.5%
Anna's Hummingbird	-0.204	0.082	-0.359	-0.037
Chestnut-backed Chickadee	-0.160	0.098	-0.247	0.033
Bushtit	-0.095	0.073	-0.240	0.050
Ruby-crowned Kinglet	0.058	0.062	-0.065	0.180
American Goldfinch	0.043	0.088	-0.138	0.216
Song Sparrow	0.015	0.068	-0.116	0.149
Bullock's Oriole	0.001	0.115	-0.227	0.225
Common Yellowthroat	-0.170	0.096	-0.360	0.019
Audubon's Yellow-rumped Warbler	-0.052	0.048	-0.145	0.040
Myrtle Yellow-rumped Warbler	-0.115	0.079	-0.272	0.038
Wilson's Warbler	-0.091	0.072	-0.231	0.051

Table A1.7. Sample sizes of the eleven taxa used in sex-based analysis. All taxa with ≥ 28 captures of individuals of known sex were included.

Taxa	Female		Male	
	Ground	Elevated	Ground	Elevated
Anna's Hummingbird	29	35	14	44
Chestnut-backed Chickadee	18	23	12	32
Bushtit	48	36	46	51
Ruby-crowned Kinglet	60	84	51	57
American Goldfinch	7	36	7	27
Song Sparrow	57	28	69	32
Bullock's Oriole	14	20	15	21
Common Yellowthroat	28	8	39	30
Audubon's Yellow-rumped Warbler	43	90	74	197
Myrtle Yellow-rumped Warbler	25	31	37	75
Wilson's Warbler	35	34	63	88

Table A1.8. Summary statistics for the posterior distributions of the difference between probabilities of aerial capture between seasons for taxa banded at the Coyote Creek Field Station, CA, from 1993-2020. A positive value indicates a greater aerial height bias in the first-listed season compared to the second-listed season. Significant differences are bolded for ease of reading as well.

Taxa	95 % Credibility Intervals for the Difference between Seasons					
	Winter – Spring	Winter – Summer	Winter – Fall	Spring – Summer	Spring – Fall	Summer – Fall
Anna's			0.047, 0.435			
Hummingbird						
Western				-0.220, 0.087	-0.178, 0.116	-0.041, 0.112
Flycatcher						
Chestnut-backed	-0.230, 0.067	-0.242, 0.056	-0.191, 0.109	-0.164, 0.147	-0.109, 0.197	-0.106, 0.197
Chickadee						
Bushtit	-0.010, 0.297		-0.206, 0.171		-0.339, 0.012	
Ruby-crowned	0.005, 0.330		-0.054, 0.194			
Kinglet						

Swainson's			0.058, 0.283	
Thrush				
Hermit Thrush	-0.057, 0.199	-0.008, 0.199	-0.083, 0.126	
American Robin	-0.299, 0.152			
Fox Sparrow		-0.128, 0.247		
Puget-sound	-0.293, 0.164	-0.244, 0.207		
White-crowned				
Sparrow				
Golden-crowned	-0.158, 0.192	-0.165, 0.192	-0.167, 0.178	
Sparrow				
Song Sparrow		0.034, 0.281	-0.188, 0.074	-0.367, -0.073
Bullock's Oriole		-0.282, 0.109		
Orange-crowned			-0.258, 0.114	
Warbler				
Common		0.037, 0.396		
Yellowthroat				

Audubon's	-0.099, 0.076	-0.153, 0.098	-0.124, 0.099
Yellow-rumped			
Warbler			
Myrtle Yellow-	-0.081, 0.166		
rumped Warbler			
Wilson's			-0.052, 0.259
Warbler			

Table A1.9. Sample sizes of the eighteen taxa analyzed across seasons. All taxa and season combinations with ≥ 28 captures were included.

Taxa	Winter		Spring		Summer		Fall	
	Ground	Elevated	Ground	Elevated	Ground	Elevated	Ground	Elevated
Anna's Hummingbird	18	20					9	32
Western Flycatcher			20	28	125	130	208	250
Chestnut-backed Chickadee	19	45	29	47	30	47	24	47
Bushtit	36	32	33	54			22	18
Ruby-crowned Kinglet	58	57	14	28			48	62
Swainson's Thrush			185	63			55	40
Hermit Thrush	65	23	71	36			202	116
American Robin	17	18	20	15				
Fox Sparrow	22	7					52	25
Puget-sound White-crowned Sparrow	18	16	17	11			21	17
Golden-crowned Sparrow	31	21	33	24			36	26

Song Sparrow			101	39	41	20	42	11
Bullock's Oriole			18	28	24	25		
Orange-crowned Warbler			37	53			18	19
Common Yellowthroat			52	21	20	21		
Audubon's Yellow-rumped Warbler	41	101	107	245			24	53
Myrtle Yellow-rumped Warbler	37	50	66	106				
Wilson's Warbler			92	103			16	29