Title: A comparison of breeding population estimators using nest and brood monitoring data

Running title: Estimating breeding population size of birds

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Abstract

1. For many species, breeding population size is an important metric for assessing population status. A variety of simple methods are often used to estimate this metric for ground-nesting birds that nest in open habitats (e.g., beaches, riverine sandbars). The error and bias associated with estimates derived using these methods vary in relation to differing monitoring intensities and detection rates. However, these errors and biases are often difficult to obtain, poorly understood and largely unreported.

2. A method was developed to estimate the number of breeding pairs using counts of nests and broods from monitoring data where multiple surveys were made throughout a single breeding season (breeding pair estimator; BPE). The BPE method was compared to two commonly used estimation methods using simulated data from an individual based model that allowed for the comparison of biases and accuracy.

3. The BPE method underestimated the number of breeding pairs, but generally performed better than the other two commonly used methods when detection rates were low and monitoring frequency high. As detection rates and time between surveys increased, the maximum nest and brood count method performs equally to the BPE.

4. The BPE was compared to four other methods used to estimate breeding pairs for empirically derived data sets on the Platte River. While the BPE was not significantly different than the other methods, it proved to provide reasonable estimates that were near the median of the other estimators combined.

5. When data from multiple nest and brood surveys are available, the BPE appears to result in reasonable estimates of numbers of breeding pairs. When survey data exceeds 14 days, the maximum nest and brood count method was statistically indifferent from the BPE. Regardless of the estimation method, investigators are encouraged to acknowledge whether the method employed is likely to over or underestimate breeding pairs. This paper provides a means to address that uncertainty.

Key Words: BPE, breeding pair, breeding population size, breeding population estimator, *Charadrius melodus*, ground-nesting birds, interior least tern, piping plover, Platte River, S*ternula antillarum athalassos*, threatened and endangered species.

Introduction

For threatened or endangered birds, breeding population size is an important metric for assessing recovery of the species. If the method(s) used to estimate the size of breeding populations are not well documented, population estimates may be dissimilar and not comparable across subpopulations or within a single population over time. For example, a review of several recovery plans, biological opinions, monitoring protocols, and reports focused on endangered interior least terns (*Sternula antillarum athalassos*; least tern) and threatened piping plovers (*Charadrius melodus*) found most of these documents recommend estimating the numbers of breeding pairs within localized areas where nesting occurs (hereafter "subpopulations"). In these documents, methods for estimating the number of breeding pairs in the subpopulations included a range of methods, but no specific recommendations (Hecht and Melvin 2009; Environment Canada 2013; Shaffer et al. 2013); included multiple methods to be employed within or between nesting seasons and therefore may not be comparable across nesting seasons (Platte River Recovery Implementation Program [Program] 2011; Frost 2013, Shaffer et al. 2013); or, in a large number of cases, were not defined and left to be chosen by the investigator (U.S. Fish and Wildlife Service [USFWS] 1988, 1989, 1990, 1996, 2003, 2006; U.S. Army Corps of Engineers [USACE] 1993, 1999; Whitfield et al. 1996; Lutey 2002; Boettcher et al. 2007). Recovery plans for other ground-nesting bird species may suffer from similar ambiguities.

The review revealed that the methods most commonly used to estimate breeding pairs included: maximum annual adult count / two; adult count during a single standardized survey / two (e.g., mid-June); numbers of active nest and broods observed during a single survey; and total numbers of nests observed (Burger 1984, 1988; USACE 1993; Environment Canada 2006, Program 2011; USFWS 2011; Frost 2013; Shaffer et al. 2013). To produce reliable estimates of breeding pairs, each of these methods require implicit assumptions. However, these assumptions may not be appropriate given the monitoring data and associated data collection protocols. As a result, comparisons of breeding pair estimates between subpopulations or through time can be unreliable and potentially misleading when the assumptions of the methods are not met. As a result, evaluations of recovery status (e.g., the number of breeding pairs in a subpopulation) using these methods can be misleading.

To date, development and evaluation of methods for estimating the number of least tern and piping plover breeding pairs in a subpopulation has been lacking. This study focused on development and evaluation of a method that uses nest and brood monitoring data, which many monitoring programs record as a normal part of monitoring efforts. The objective of our study was to describe and evaluate a method (hereafter breeding pair estimator; BPE) for estimating breeding population size using nest and brood monitoring data. The resulting BPE method is described in detail. The performance of the BPE is then evaluated against other commonly used methods using real and simulated data.

Methods

DATA REQURIMENTS FOR BREEDING PAIR ESTIMATOR

Our BPE assumes the number of active nests $n(t)$ and broods $b(t)$ within the population is known or estimable at any given time (t) during the nesting and brood rearing season (T; using parenthetical indexing notation to represent continuous time). Such data can be obtained using a variety of survey techniques such as distant observations, aerial surveys, and grid searching. Ideally, the survey technique would be able to determine the number of active nests and broods within the system on a near continuous basis. In reality, these data are typically collected at discrete points in time (i.e., t = 1, 2…) where it can only be assumed to approximate the continuous process. Consequently, the precise date and time nests and broods are initiated, hatch, fail, or fledge is rarely known. Therefore the time when transitions in $n(t)$ and $b(t)$ occur is unknown. In order to transform the observed discrete data into reasonable approximations of the continuous process, the following six assumptions are used to determine the date events occurred:

1) The initiation date of successful nests (i.e., ≥1 egg hatched) was calculated using the maximum between the period the nest was observed to be active and a known amount of time that must pass between when a nest was initiated and when ≥1 egg hatched (hereafter referred to as the nest interval). A reasonable estimate of the nest interval can be obtained from the literature or from auxiliary data (e.g., band resightings).
2) The initiation date of failed nests was assumed to have occurred on the date the nest was first observed. Nest and brood monitoring data do not contain information that would allow for a meaningful calculation of the nest initiation date. As such, nests with a final fate of failed or unknown were assumed to be initiated on the day they were first observed.
3) Nest or brood hatching, failure, or fledging events that occurred between surveys were assumed to have occurred at the midpoint between visits. By using the midpoint between successive observations, the timing of each event was overestimated and underestimated with equal chance (Mayfield 1961; Johnson 1979; Schroeder 1997).
4) The date ≥1 chick fledged from of a brood was calculated using a known amount of time that must pass between when a nest hatched ≥1 egg and when ≥1 chick fledged

(hereafter referred to as the brood interval). Reasonable estimates of the brood interval could be obtained from the literature.

5) The minimum amount of time that must pass before a breeding pair with a failed nest or brood can initiate another nest was known (hereafter referred to as the renest interval). The renest interval can be determined from the literature or from auxiliary data (e.g., band resightings).
6) The minimum amount of time that must pass before a breeding pair that fledges a brood can initiate another nest was known (hereafter referred to as the post-fledge interval). This can be determined from the literature or auxiliary data. For species that produce only one brood per seasons (e.g., least terns), the post-fledge interval will be the time period from when the brood fledges until the end of the nesting season.

A visual example of the requisite data is provided (Fig. 1).

BREEDING PAIRS ESTIMATOR

Using the data and assumptions described above, breeding pair estimates were based on the sum of active nests and broods and failed nests and broods with renest intervals that extend through time *t*, and hatched broods with post-fledge interval extending through time *t* for each day of the nesting season (i.e., the assumed time step is 1 day; Fig. 1). Numbers of breeding pairs were calculated using the estimator

$$\widehat{N} = \max_{t \in T}\{n(t) + b(t) + r(t) + f(t)\} \qquad \text{(eqn 1)}$$

where $\widehat{N}$ is the estimated number of breeding pairs, $n(t)$ is the number of active nests, and $b(t)$ is the number of broods on the t^{th} day. The $r(t)$ is the number of failed nests or broods with renest intervals extended thought the t^{th} day and $f(t)$ is the number of fledged broods with post-fledge intervals extending through the t^{th} day. The notation $t \in S$ simply states the t^{th} day occurs "within" the nesting and brood rearing season T. This estimator assumes $n(t)$ and $b(t)$, and by extension $r(t)$ and $f(t)$, are known without error, which means the number of nests and broods counted during any given survey period can reasonably be assumed to be a census (see Simulation Experiment below for a test of this assumption). Annual estimates of breeding pairs are obtained by identifying the maximum of $n(t) + \ b(t) + r(t) + f(t)$ for any given day during the nesting and brood rearing season (Fig. 1). To assist users, a tutorial and an excel spreadsheet are provided to assist in implementation of the BPE method (Appendices S1–S2).

ALTERNATIVE BREEDING PAIR ESTIMATORS

One method commonly used to estimate the number of breeding pairs is maximum number of active nests n_i and broods b_i on any given survey (i; hereafter referred to as max nest and brood counts):

$$\hat{N} = \max_{i \in S}\{n_i + \ b_i\}. \qquad \text{(eqn 2)}$$

Subscript indexing notation is used to represent discrete surveys. The notation $s \in S$ states the i^{th} survey occurs "within" the discrete nesting and brood monitoring S (i.e., $i = 1,2,\ldots,s$; where s is the total number of surveys). This method does not require "continuous" data and does not require the identity of nests or broods be uniquely identified.

Another commonly used estimation methods is cumulative nest counts

$$\hat{N} = \sum_{i=1}^{s} \Delta n_i, \qquad \text{(eqn 3)}$$

where Δn_i is the number of new nests added during the i^{th} survey (except for the first survey $\Delta n_1$is the number of nest observed). This method does not require "continuous" data, but does require nests be uniquely identified.

SIMULATION EXPERMENT

TernCOLONY is an individual based simulation model that was developed to better understand how reservoir operations and management activities affect least tern breeding populations on large river systems (Lott et al. 2012 and 2013). TernCOLONY is ideal for evaluating estimation methods because the model is process based, realistic, detailed, and the "true" number of breeding pairs is known. Output from 600 individual TernCOLONY simulation runs was used to test the ability of the three methods (BPE, max nest and brood counts, and cumulative nest counts) to estimate the known number of breeding pair from each model run. Each simulation included a total of 446 adults, but arrival and departure dates of individual adults varied as did the number of adults forming breeding pairs. As a result, the number of adults was the same across all simulations, but the number of breeding pairs was variable, influenced by annual habitat conditions, and was based on the number of females that initiated ≥1 nest within the model run. In TernCOLONY, the nest period, brood period, and renest interval were variable and had a mean of 21 days, 20 days, and five days, respectively. Renesting did not occur after a female produced a successful brood (fledged ≥1 chick) in TernCOLONY.

The 600 model runs incorporated multiple combinations of nesting conditions (excellent habitat with low predation or degraded habitat with high predation) and water year (high flow, low flow, or mid-season flood) and included 30 replicates for each of the following scenarios:

1) 2 years when habitat was degraded (old), flows were high, and predation was high;
2) 4 years when habitat was degraded, flows were low, and predation was high;
3) 4 years when habitat was degraded, a mid-season flood occurred, and predation was high;
4) 2 years when habitat was excellent (new), flows were high, and predation was low;
5) 4 years when habitat was excellent, flows were low, and predation was low;
6) 4 years when habitat was excellent, a mid-season flood occurred, and predation was low.

The BPE (eqn. 1), maximum number of active nests and broods (eqn. 2), and cumulative number of nests (eqn. 3) all assume the number of nests or broods can be detected perfectly. The assumption of perfect detection is unrealistic. Because all estimation methods are sensitive to this assumption, a binomial distribution was used to simulate non-detection of nests and broods. In addition, estimates from each method are sensitive to sampling interval (i.e., how frequently data are collected). Each model run was sampled every third, seventh, and fourteenth day and once during the season (June 15) assuming a detection probability of 0.50, 0.75 and 1.00. This data was then used to estimate breeding pairs using the BPE (eqn. 1), maximum number of active nests and broods (eqn. 2), and cumulative number of nests (eqn. 3).

The BPE model assumptions included a nest interval of 21 days, a brood interval of 20 days, a renest interval of five days and a post-fledge interval extending to the end of the nesting season (i.e., renesting did not occur after producing a successful brood). Results of the BPE are presented as $\widehat{N}$ divided by the known number of breeding pairs for each model run with all scenarios combined (see Fig. 2). Ratios of 1.00 represents a perfect estimate of the known number of breeding pair and values above or below 1.00 indicate over or under estimates of breeding pairs, respectively.

Case Study

BACKGROUND

The case study used data from the Associated Habitat Reach (AHR) of the central Platte River Valley beginning at the junction of U.S. Highway 283 and Interstate 80 near Lexington, Nebraska, and extending eastward to Chapman, Nebraska, USA (Program 2006, 2011). The AHR provides breeding habitat for a variety of shorebirds, including the federally endangered least tern and threatened piping plover (Faanes 1983; Sidle and Kirsch 1993; Jenniges and

Plettner 2008). Throughout their range, least terns and piping plovers nest sympatrically on in-channel (sandbars), off-channel (sand and gravel mines), and shoreline nesting habitats (Ziewitz et al. 1992; Jenniges and Plettner 2008).

The study area represents a sub-population of least terns and piping plovers that occur along the central Platte River in Nebraska. Many areas within these species' ranges are surveyed to count and monitor nests and broods which results in data similar to data collected in the AHR. Throughout the species' range, at least eight methods are used to calculate numbers of breeding pairs (USACE 1993; Program 2011; USFWS 2011; Frost 2013; Shaffer et al. 2013). At the moment, it is unclear how reported counts using such disparate methods can be reconciled to determine the status of the breeding populations.

FIELD SURVEY TECHNIQUES

The least tern and piping plover monitoring protocol implemented in the AHR from 2001–2014 was comprised of two main components: 1) semi-monthly river surveys and 2) semi-monthly surveys of historic, existing, and potential sandpit nesting sites within the AHR (Program 2011). During these surveys, numbers of adults, nests, and chicks of each species observed were recorded. Nests and broods located during surveys were monitored at least twice per week as long as nests or broods were present and new nests and broods were located during each survey. The frequency of survey and monitoring efforts (twice weekly) allowed detection of a large, but unknown proportion of nests within the AHR and allowed the derivation of fairly accurate estimates of the timing of nest or brood failures as well as hatching and fledging events. The data required to estimate the number of breeding pairs using BPE along with calculations used in the BPE are available in a spreadsheet archived on the Dryad Digital Repository (see Data Accessibility; Appendix S2).

BREEDING PAIR ESTIMATE AND COMPARISON

Monitoring data collected in the AHR was used to compare five methods of estimating breeding pairs annually: BPE (eqn. 1), cumulative nest counts (eqn. 3), maximum number of nests and broods observed during mid-month and semi-monthly surveys (eqn. 2), number of nests and broods observed on 15 June (eqn. 2 with a single sample period), and half of the maximum number of adults observed during mid-month and semi-monthly surveys of the AHR. The last method (half of the maximum number of adults) was included because it is a common method used to estimate the number of breeding pairs in the study area and is currently used for other subpopulations. We define 'nesting period' as the time a nest was first initiated (first egg in the scrape) to the time when the nest hatched. We are fully aware the 'nesting period' could be as much as 24 – 26 days from when a nest is initiated to when it hatches, however, our goal was to develop a method that was conservative, but yet a reasonable estimate of the number of breeding pair in the AHR.

Annual least tern and piping plover breeding pair counts were estimated using eqn. 1, which required calculations of $n(t)$, $b(t)$, $r(t)$, and $f(t)$ for each species and day of the nesting seasons. The BPE assumptions for least terns included a nest interval of 21 days (incubation period), a brood interval of 21 days, a renest interval of five days and a post-fledge interval that extended to the end of the nesting season (i.e., no renesting after successfully fledging a brood). The renest interval of five days was based on band-resight data, observations of nesting chronology, and published data (Massey and Fancher 1989; Lingle 1990 and 1993; Lott et al. 2012; Program unpublished data). The BPE assumptions for piping plover included a nest interval of 28 days, a brood interval of 28 days, a renest interval of five days, and a post-fledge interval of five days. The renest and post-fledge intervals were based on band-resight data, observations of nesting chronology, and published data (Roudybush et al. 1979; Amat et al. 1999; Shaffer et al. 2013; Program 2014).

An important goal of the Program monitoring protocol is to detect population trends. Simple linear regression was used to detect trends in the time series of 2001–2014 data based on the breeding pair estimates. Regression coefficient and associated 95% CIs were reported. A pair-wise correlation matrix was also developed for each estimation method for comparison purposes.

Results

SIMULATION EXPERIMENT

The BPE and maximum nest and brood count methods usually resulted in statistically indistinguishable breeding pair estimates negatively biased (underestimated) under all sampling intensities and detection rates except for the 3-day sampling with perfect detection. The magnitude of the negative bias depended on the sampling interval and detection rates (Fig. 2). The cumulative number of nests method typically overestimated the number of breeding pairs when sampling occurred frequently (3-day and 7-day) and underestimated when sampling occurred less frequently. As with the other methods, the magnitude of the bias depended on the detection rate (Fig. 2). When detection was low and only a single mid-June survey was simulated, estimates of the known breeding pair count were severely underestimated (negatively biased) regardless of the estimation method. This result was not unexpected as it would be highly unlikely that all nests and broods would be present during any single survey date.

Of the three methods tested, the BPE was influenced the least by detection rates. The BPE was most sensitive to sampling interval when detection was low (i.e., 50%) and estimates improved as detection increased to 100%. When detection was high and the sampling interval was short (i.e., 3-day sampling interval), the BPE resulted in an average breeding pair estimate that was 18% (range = 16% – 21%) less than the true value. By design, estimates from the BPE and maximum nest and brood count methods were identical when only a mid-June survey was simulated.

Estimates of breeding pair counts derived using the maximum nest and brood count method were also most often underestimated. The maximum nest and brood count method was the least influenced by sampling intensity of all methods tested (Fig. 2). Results of the maximum nest and brood count method were indistinguishable from the BPE when detection was assumed to perfect. When detection was low, this method typically resulted in the most negatively biased estimates (underestimated) of all methods tested (54% to 71% low).

The cumulative nest count method produced breeding pair counts that ranged from highly overestimated (+53%) to highly underestimated (–72%). Results of this method were highly dependent on the survey interval and detection rate. Estimates obtained from cumulative nest counts were most exaggerated (overestimated) when the sampling interval was short and detection was high and declined as the sampling interval increased and detection decreased. When detection was perfect, the cumulative nest count method overestimated the known breeding pair counts by 24% – 53% when multiple surveys were implemented. When detection was perfect and only a single sampling interval was used to obtain estimates, breeding pair counts were underestimated (–43%).

CASE STUDY

Trends in AHR least tern breeding pair estimates were positively correlated and tended to follow a similar increasing pattern for all nest and brood monitoring methods tested (Table 1; Fig. 3). Regression coefficients for the trend line associated with each method varied from 1.35

(Adult count/2) to 5.55 (cumulative nest counts). The 95% CIs for all trend lines, however, overlapped indicating the regression coefficient for all five methods could be the same (Table 1). As with the simulation experiment, least tern 15-June nest and brood counts provided the lowest estimate of breeding pairs. Maximum nest and brood counts obtained from mid-month (2001–2009) and semi-monthly (2010–2014) surveys were highly correlated with BPE (r=0.96). Cumulative nest counts generally provided the highest annual estimates of breeding pairs. However, it is known that this method would always be biased high unless all breeding pairs only produced a single nest each year.

Similar to least terns, trends in piping plover breeding pair estimates tended to follow a similar increasing pattern for all methods tested (Table 1; Fig. 4). Regression coefficients for the trend line associated with each method varied from 1.24 (15 June nest and brood counts) to 1.97 (cumulative nest counts). The 95% CIs for all trend lines overlapped indicating the regression coefficient for all five methods could be the same (Table 1). Adult piping plover counts tended to be most comparable to breeding pair estimates generated by the BPE. The 15-June nest and brood count and maximum mid-month and semi-monthly methods for piping plovers resulted in similar estimates; however, these methods were at times up to 47% lower than the BPE for estimating breeding pairs. The cumulative nest count method provided the highest annual estimates of breeding pairs and at times was 53% (range 10% – 53%) higher than the BPE.

Discussion

SIMULATED EXPERIMENT

In TernCOLONY simulations, nest and brood counts were perfectly observable in nearly continuous time with no error. The performance of three breeding pair estimation methods was compared by sampling from the simulated populations. This allowed for comparison of bias across methods relative to perfect knowledge of the population. Many papers have addressed the ubiquitous problem of imperfect detection in wildlife surveys (Thompson 2002; Lott 2006). In this analysis, detection rates were varied from 50% to perfect detection (100%) and sampling interval from a single survey to a 3 day sampling interval. Length of the interval between sampling periods to a given nesting area can bias detection toward successful nests, potentially leading to underestimates of initiated nests and nest loss rate and an inability to quantify causes of nest loss (Shaffer et al. 2013). Incorporating detection rates and sampling interval into the analysis allowed quantification of the sensitivity of breeding pair estimation methods to these known issues.

The BPE is a method developed by the Program to estimate the number of breeding pairs using nest and brood monitoring data that includes a rest period between lost nests or broods and renesting by an individual pair. Though the method employed by Shaffer et al. (2013) was similar to the BPE that has been used in the AHR for several years, the minimum breeding population (MINBPOP) method does not account for breeding pairs that renest after losing a nest or brood. Thus, the implication of this is that results of the MINBPOP method are identical to the cumulative nest count method used in our study as every nest counted was assumed to be associated with a unique breeding pair. We feel the BPE will be most useful for breeding bird populations that nest in open habitats (e.g., sandbars, beaches, etc.) for which numbers of nests and broods counted on any given sampling period can reasonably be assumed to be high, but less than perfect (i.e., detection <100%). Results from the simulation study show the BPE tended to produce the most unbiased and least variable estimate of the total number of breeding pairs in a population so long as sampling occurred fairly frequently (i.e., 3-day interval) and detection was assumed to be imperfect. Though variable, estimates across individual nest and brood monitoring methods at the similar levels of detection and sampling interval tested were statistically indistinguishable.

In many cases, the primary goal may be to estimate the number of breeding pairs in the population. Another goal may be the development of an index of breeding pair abundance that is comparable across different study areas and sampling intensities or designs. For example, the sampling intensity (e.g., 3-day, 7-day, etc.) may vary over time due to availability of funding within a study area. If the goal was to produce an index that is comparable when sampling interval is variable, then the maximum nest and brood count method appears to be less sensitive to a variable sampling interval; however, estimates were consistently lower than the known number of breeding pairs and estimates obtained by the BPE.

CASE STUDY

An illustrative example was provided using monitoring data for least terns and piping plovers collected in the AHR to evaluate management actions for a large scale species recovery program. Recovery plans require numbers of pairs to be estimated to determine if recovery goals have been met. If pair estimates are used to estimate trends, all five methods produced coefficient estimates that indicated the subpopulation within the AHR was increasing and, based on overlapping CIs, coefficients obtained from all breeding pair estimation methods were not statistically different.

Though recovery goals for least terns and piping plover are based on maintenance of pairs of each species in subpopulations for a predetermined time period, recovery plans provide no guidance for how pairs are to be determined. Although we evaluated multiple disparate methods of estimating breeding pairs, our analyses indicated there were no statistical differences between methods in regards to estimating trends in the population (Table 1). When comparing regression coefficients for least terns, however, the maximum nest count and the adult count methods resulted in estimates of slope that were more than four times greater for the maximum nest count method. However, our inability to detect a difference between methods was due to the high variability in counts over time.

If adult counts are to be used to determine numbers of pairs, we feel it is important to acknowledge and attempt to account for several factors including some adults are not actively paired during the nesting season, obtaining accurate counts of adults may be difficult in large colonies, assessing detection rates for adults may be difficult given their high mobility and foraging behaviors, and similar to the cumulative nest count method, adult counts have been reported to result in breeding pair estimates that range widely from overestimated to underestimated (Sherfy et al. 2012, Shaffer et al. 2013). We were not able to estimate breeding pair counts in our simulation study and therefore cannot provide any guidance as to how this method compares to nest-based methods used in our study. However, we feel it is safe to assume more adults would equate to more breeding pairs and thus using the adult count method to estimate trends in breeding pair counts likely would result in a similar pattern as using other methods (Figures 3 and 4).

In the AHR and other areas, least terns and piping plovers nest on bare sand habitat provided on in-channel sandbars and off-channel sand and gravel mines (Program 2012, 2014). Given high intensity monitoring (e.g., at least twice weekly) and characteristics of habitat used by least terns and piping plovers (bare sand), we suspect detections rates in the AHR are high and believe nest and brood counts can be assumed to approximate a census (Roche et al. 2014). If this is the case, the BPE and maximum nest and brood count methods result in estimates of breeding pairs that were indistinguishable. The assumption of perfect detection, however, should be justified based on the ecology of the species studied and survey methodology employed. If information about the detection process and rate for nests and broods is available (e.g., Roche et al. 2014), the BPE could easily be extended to incorporate this information. For example, one could use the estimated probability of detection of nests and broods to adjust the number of nests and broods that are active on a given day ($n(t)$ in eqn 1). For example, assuming a detection rate of 75% and given the high intensity sampling that occurs within the AHR, results of our simulation indicate estimates of breeding pairs derived using the BPE may in fact be approximately 18% lower than reality.

Conclusion

All methods examined resulted in estimates of numbers of breeding pairs that were not significantly different, however, this was likely due to the variability in the data as difference between estimates were as much as fourfold. Thus, the need a unified approach for estimating these metrics throughout a species' range is evident. A unified approach would allow for direct comparisons of breeding pair counts and productivity measures (fledge ratios, etc.) between regions where a species nests, so long as the nesting and brood rearing period were defined in a similar manner. When nest and brood monitoring data are collected at intervals of less than 14 days, the BPE provided estimates of breeding pairs that were the most precise and accurate, especially when detection was assumed to be less than perfect. If survey intervals exceed 14 days and detection can be assumed to be nearly perfect, the maximum nest and brood count method results in estimates that were generally conservative (underestimate breeding pairs), but indistinguishable from estimates produced by the BPE. The cumulative nest count method is highly sensitive to monitoring intervals and results in breeding pair estimates that range from highly under estimated to highly over estimated. We recommend practitioners refer to the simulation portion of this analysis to develop a better understanding of the sensitivity of currently used estimators to monitoring frequency and detection and whether or not those estimators are likely to over or under estimate breeding pairs. We also recommend researchers enter nest and brood monitoring data into a standardized database, such as Appendix S2, so comparable assumptions and estimates can be derived throughout the study species' range.

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Data accessibility

The source data for the tern and plover estimation exercises are archived in the Dryad Digital Repository doi:XXX.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Tutorial for using Appendix S2 to implement Breeding Population Estimator (BPE).

Appendix S2. Excel Spreadsheet for implementing our Breeding Population Estimator (BPE).

Appendix S3. Figure S1.

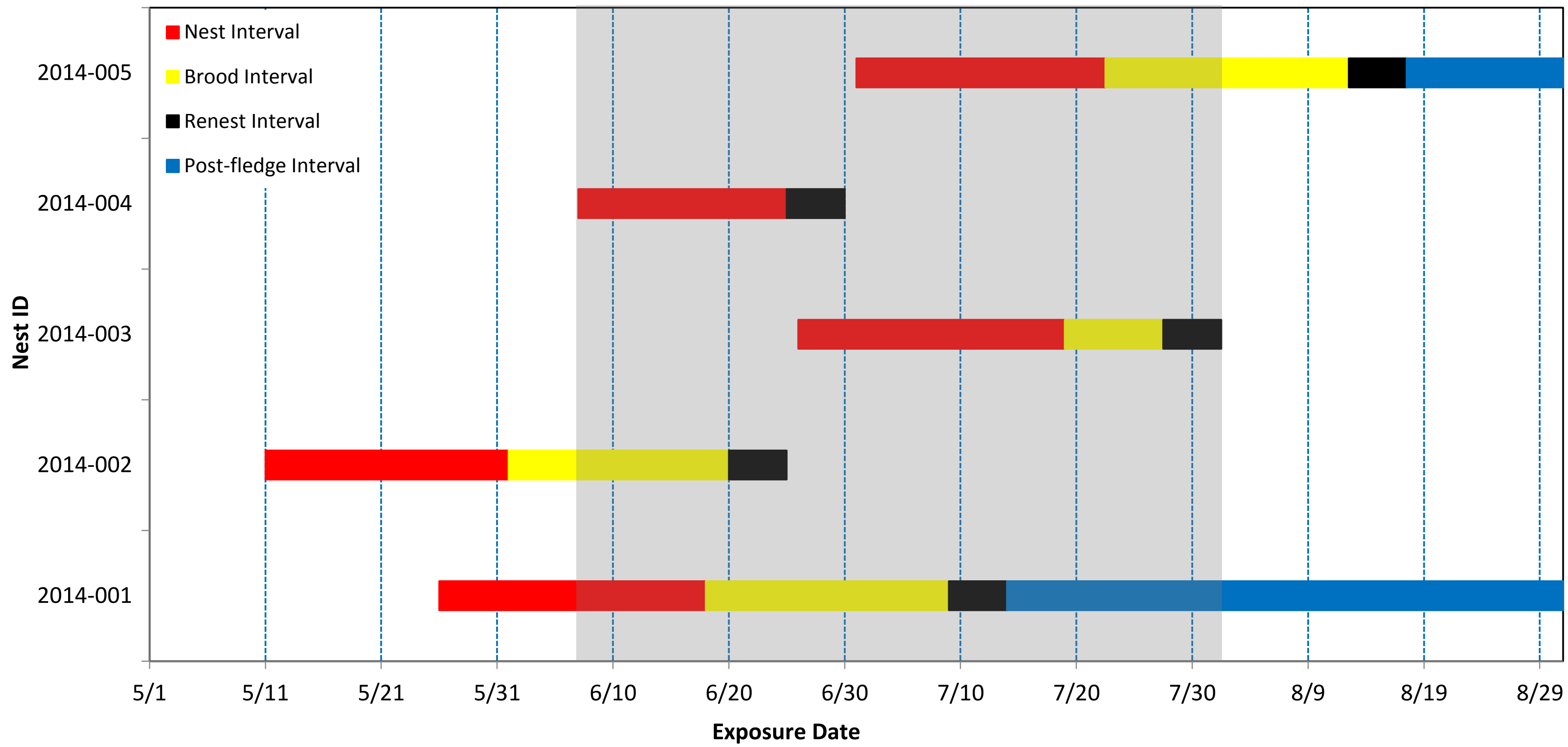

Figure 1. Example showing how nest and brood monitoring data and a user-defined nest interval (21 days), brood interval (21 days), renest interval (five days) and post-fledge interval were used to estimate breeding pairs. In this example the post-fledge interval extends from the time a brood fledged to the End of Breeding Season (EOBS) as the species in this hypothetical example did not renest after fledging a brood (blue bars extending to the right side of the renest interval). The grey shaded area indicates when the maximum numbers of breeding pairs (three) occurred. The vertical dashed blue lines represent a hypothetical sampling interval that occurred every 10 days. The Breeding Population Estimator (BPE) assumes sampling occurs at sufficient regularity that the maximum number of breeding pairs can reliability be estimated.

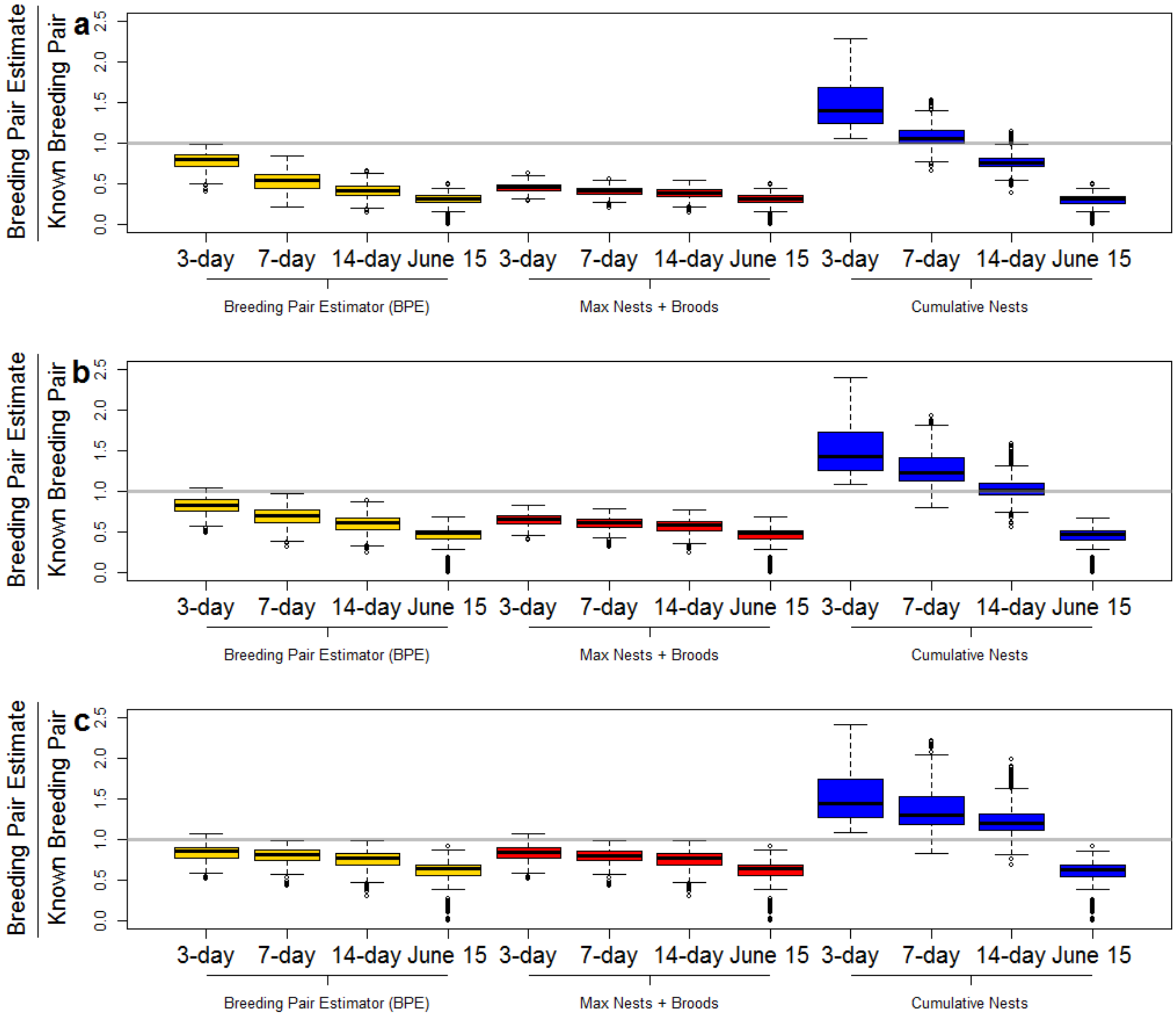

Figure 2. Evaluation of three estimation methods for determining the number of breeding pairs of least terns using simulated data produced by TernCOLONY. Values of 1.0 (grey line) indicate perfect estimates of the known breeding pair count. The sampling interval was varied from every third day (3-day) to once per nesting season (June 15). The detection rate was 0.50 (**a**), 0.75 (**b**) and 1.00 (**c**).

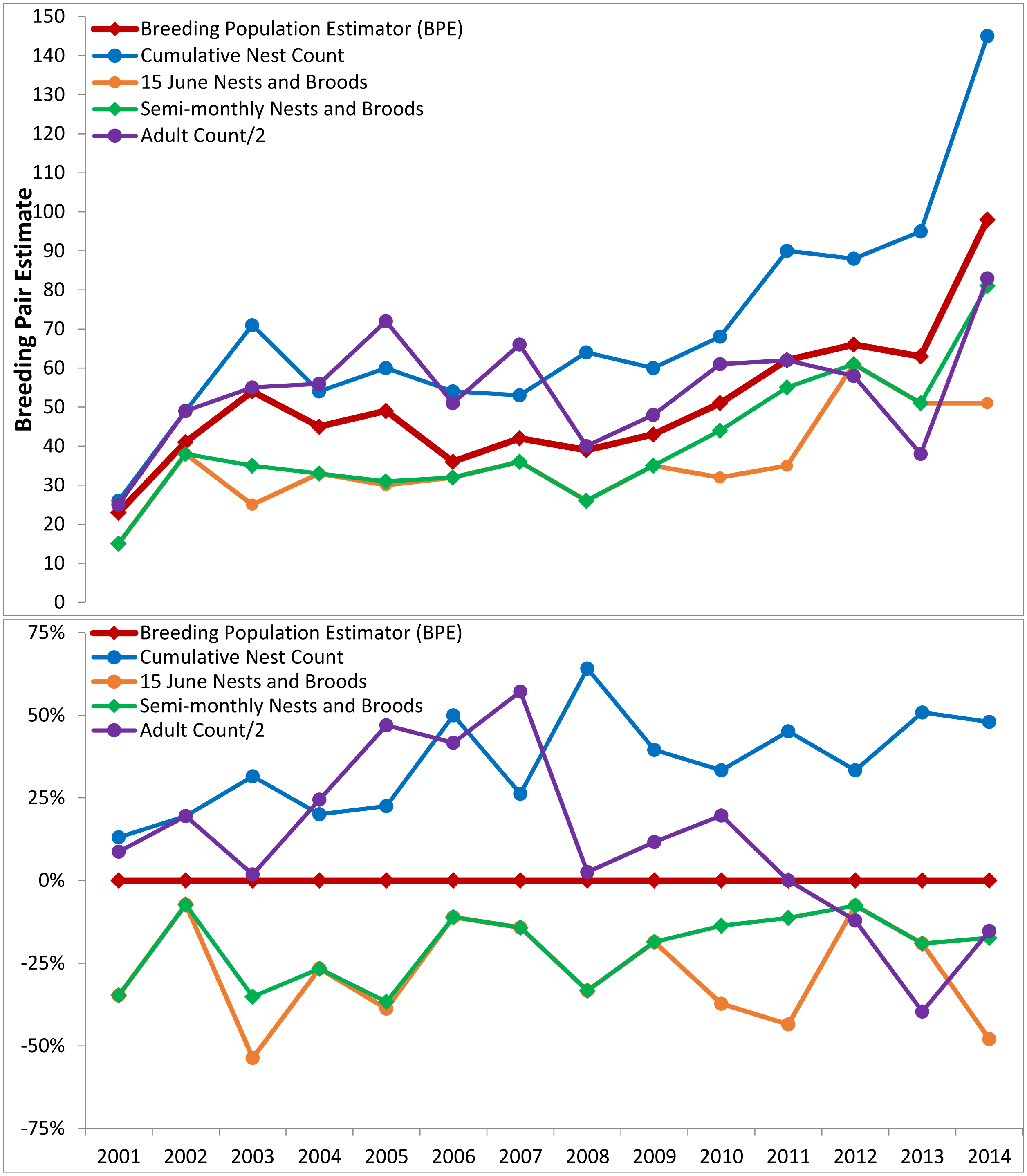

Figure 3. Five estimates of least tern breeding pairs within the central Platte River Valley (top). An evaluation of how each estimate compares to estimates from our breeding pair estimator (BPE; bottom). The comparison in the bottom plot was calculated as (*x*-BPE)/BPE, where *x* is the estimate obtained using one of the four other methods.

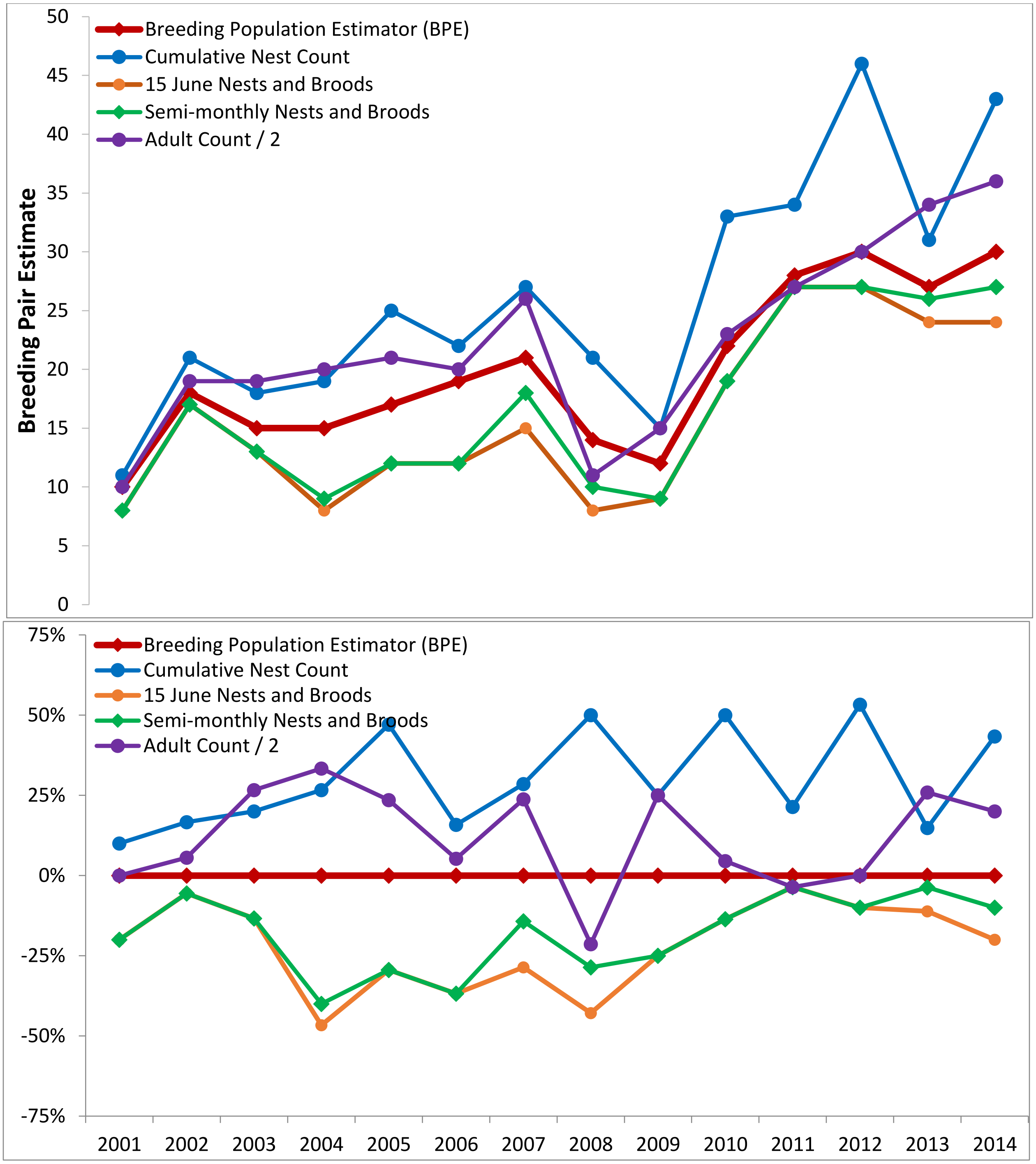

Figure 4. Five estimates of piping plover breeding pairs within the central Platte River Valley (top). An evaluation of how each estimate compares to estimates from our breeding pair estimator (BPE; bottom). The comparison in the bottom plot was calculated as (*x*-BPE)/BPE, where *x* is the estimate obtained using one of the four other methods.

Table 1. Regression coefficient and 95% confidence interval (CI) from a trend analysis of various breeding pair estimates obtained from data of least terns and piping plovers, 2001–2014. Also reported for comparison purposes is the pair-wise correlation matrix between each estimation method.

Estimator	Regression Coefficient (95% CI)	Correlation				
		BPE	Cumulative Nest Counts	15 June Nests and Broods	Semi-monthly Nests and Broods	Adult Count/2
Least terns						
Breeding pair estimator (BPE)	3.24 (1.48–4.99)	1.00	0.98	0.73	0.96	0.67
Cumulative Nest Counts	5.55 (3.13–7.98)		1.00	0.70	0.94	0.58
15 June Nests and Broods	2.11 (0.92–3.29)			1.00	0.83	0.40
Semi-monthly Nests and Broods	3.19 (1.73–4.66)				1.00	0.63
Adult Count/2	1.35 (-0.69–3.38)					1.00
Piping plovers						
Breeding pair estimator (BPE)	1.28 (0.68–1.88)	1.00	0.95	0.95	0.97	0.93
Cumulative Nest Counts	1.97 (1.06–2.87)		1.00	0.88	0.90	0.86
15 June Nests and Broods	1.24 (0.50–1.98)			1.00	0.99	0.85
Semi-monthly Nests and Broods	1.35 (0.64–2.07)				1.00	0.90
Adult Count/2	1.39 (0.61–2.17)					1.00