

## Breeding pair and reproductive estimates of a recently expanded Red-necked Grebe (*Podiceps grisegena*) population in parkland Manitoba

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### Abstract

Conservation of wildlife populations requires reliable information on population size, trends, and demographic processes. Such information is sparse for Red-necked Grebe (*Podiceps grisegena*), a species that is vulnerable to changing wetland conditions in the prairie pothole region. During 2008–2019, I collected breeding pair and reproductive estimates of a recently expanded Red-necked Grebe population on 109 semi-permanent and permanent wetlands (mean  $\pm$  SE:  $2.92 \pm 0.41$  ha, range 0.01–24.2) in agriculturally-dominated habitat in southwestern Manitoba, Canada, to determine population status and reproductive success. I also looked for effects of changing wetland water levels and the presence of conspecifics and/or wetland size on productivity. Red-necked Grebe breeding densities were the highest reported for solitary-nesting pairs in North America and the breeding population currently appears to be stable. I found that chicks/breeding pair are mostly lower but chicks/successful pair are similar or greater than values reported from other studies. Pairs breeding with conspecifics appeared to be as productive as those on single-pair wetlands. Productivity was positively associated with wetland water levels suggesting that prolonged drought or climate change leading to warmer, drier summers on the prairies could reduce Red-necked Grebe breeding populations.

Key words: Red-necked Grebe; reproductive estimates; breeding densities; population; wetland water levels; Manitoba

### Introduction

Red-necked Grebe (*Podiceps grisegena*) is a highly-specialized, wetland-obligate species that nests over-water in or near emergent vegetation on semi-permanent or permanent ponds. In North America, they usually occupy wetlands greater than 2 ha (Fournier and Hines 1998; Stout and Nuechterlein 2020). Males and females are similar in appearance and difficult to distinguish in the field. They are intra- and interspecifically territorial. Their distribution is Holarctic and, in North America, the breeding range extends from northwestern Ontario and the northern United States to the Northwest Territories and Alaska (Fink *et al.* 2020; Stout and Nuechterlein 2020). Breeding Bird Survey (BBS) data (% change per year; 1970–2019) indicate that Red-necked Grebe populations are stable in Canada, decreasing in Alberta potholes (–4.08%), and increasing in Saskatchewan (15.9%) and Manitoba (7.11%) potholes (Smith *et al.* 2020).

However, the reliability of BBS data in all geographic regions in Canada is considered medium to

low due to small sample sizes; the lack of reliable, long-term reproductive data also hampers our understanding of this species population trajectory and environmental factors affecting reproductive rates. In agriculturally-dominated pothole habitat in southern Manitoba, an area where recorded historical populations were very low or nonexistent, Red-necked Grebes have recently experienced dramatic population growth (Hammell 2017). Field studies of Red-necked Grebe reproductive rates in the parkland ecoregion are few and not recent (see summary in Stout and Nuechterlein 2020), and to my knowledge, none focussed on the agriculturally-dominated pothole habitat in Manitoba or Saskatchewan. Furthermore, Red-necked Grebe population size, trends, and demographic processes are poorly understood (Stout and Nuechterlein 2020).

Accordingly, from 2008 to 2019, I opportunistically collected Red-necked Grebe breeding pair and brood data while conducting other waterfowl studies to determine baseline breeding pair and productivity data (broods/breeding pair, number of chicks/

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successful pair or breeding pair) for this recently expanded population in an agriculturally-dominated landscape in southern Manitoba. These data were used to assess (i) if the population was still expanding or had reached stability, (ii) if changing wetland water levels affected productivity, and (iii) if the presence of conspecifics and/or wetland size affected productivity. Reproductive rates in an agriculturally-dominated landscape may differ from those in less disturbed areas such as forested provincial parks (De Smet 1987) or the Taiga Shield ecoregion in the Northwest Territories, Canada (Fournier and Hines 1998). This has been attributed to anthropomorphic effects such as machinery (farm and recreational) and/or cattle disturbance (Wheeler 2001; Riske 1976 and Ohanjanian 1986 as cited in Stout and Nuechterlein 2020), nest loss from increased wave exposure in open landscapes (Nuechterlein *et al.* 2003), more diverse (Bayne and Hobson 1997) or differing predator community (e.g., absence of Raccoon [*Procyon lotor*] at higher latitudes, C. Wood pers. comm. 6 January 2020), or decline of aquatic vertebrate and invertebrate prey from pesticide and herbicide use in surrounding cultivated fields (Relyea 2005; Sura *et al.* 2012; Morrissey *et al.* 2015).

### Study Area

I conducted surveys in the parkland pothole region near Erickson, Manitoba (50°30'N, 99°55'W). The intensively studied areas constitute a 6.8 km<sup>2</sup> block and a 15.8 km<sup>2</sup> roadside transect (21.7 km × 0.4 km on either side of the road), 4.0–12.5 km to the southeast (see Hammell 2016 for map of study areas). The transect was established in 2009 as preliminary data collection in 2008 indicated that the block area was too small to provide adequate sample sizes (Hammell 2014). The combined block and transect areas (22.6 km<sup>2</sup>, hereafter, the primary study area) contained 97 (mean ± SE: 2.74 ± 0.45 ha, range 0.01–24.2) semi-permanent and permanent wetlands (class IV and class V; Stewart and Kantrud 1971) that required walking and driving to survey. Most years, additional pair success and brood size data were collected from 12 other, easily-accessible wetlands near the primary study area (4.3 ± 0.92 ha, range 0.9–9.5). Pair estimate and brood search protocols there were similar to those on the primary study area.

The uplands in the Erickson area are a mixture of lands sown to cereal and oilseed crops, hay, pasture, and native woodland. During 2009–2019, the approximate land use pattern for the primary study area was 25% cultivated, 34% pasture, 17% hayland, 15% wetland, 5% woodland, and 4% other (yard sites, ditches, commercial, etc.). Only one permanent small island occurred in a wetland on the block area and none on

the transect. The area and changes to the landscape over time are described in more detail by Sunde and Barica (1975) and Hammell (2014).

### Methods

#### Pair surveys

Because Red-necked Grebes require relatively deep (>1 m) wetlands with open water for breeding (Stout and Nuechterlein 2020), I restricted my observations to ponds equal to or greater than class IV (Stewart and Kantrud 1971). Red-necked Grebes are thought to attain full nuptial plumage at one-year old, but some adults may not breed until older (Stout and Nuechterlein 2020). The number of non-breeding Red-necked Grebes observed on breeding ponds is assumed to be low (Riske 1976 as cited in Stout and Nuechterlein 2020). Thus, I assumed that all birds observed represented members of breeding pairs and that there were no non-breeding pairs. Territory establishment and initial egg-laying occurs in May in Manitoba (De Smet 1987), and counts taken during mid- to late May would best represent the breeding population (Stout and Nuechterlein 2020; G.S.H. pers. obs.). Red-necked Grebes were recorded as pairs or single birds (representing a probable pair). Many pairs occurred on some larger lakes so long observation times (to 0.5 h) were necessary to estimate numbers. Repeated total counts from several elevated viewpoints, combined with field maps of bird locations (to determine territories), aided estimation.

Pair surveys were conducted from 2008 to 2018 approximately once per week from mid-May to mid-June with three to four visits to each of the 109 wetlands on the primary ( $n = 97$ ) and nearby-wetland study area ( $n = 12$ ). In 2019, visits were reduced for some wetlands (two visits one week apart). All wetlands were scanned with binoculars and spotting scopes from one or more elevated locations between 0530 and 1800. Block area wetlands were surveyed by walking a fixed route, whereas transect wetlands were surveyed from the road except distant or hidden wetlands were walked to and viewed from several locations. All wetlands with observable water (classes IV–V) within 400 m of the road were included in the transect survey, which took 17 h to complete over two days (except during 2009 and 2010, when only ~60% were surveyed). Some wetlands were bisected by the roadside transect; thus, with the exception of one large lake where I recorded pairs and broods on the “within” section of the transect only, I recorded pairs on the entire wetland and included this total in the transect pair count.

Unlike other grebes (e.g., Horned Grebe [*Podiceps auritus*] and Pied-billed Grebe [*Podilymbus podiceps*]) breeding in Manitoba, when disturbed, Red-

necked Grebes usually remain visible to the observer in open water on the surface. If they are not obvious at arrival, usually one or both pair members swim out from emergent vegetative cover after a short time (G.S.H. pers. obs.). Therefore, recorded pair estimates were considered reasonably accurate.

#### Brood surveys

I recorded number of adults, number and age of chicks, and used information about brood age, size, and location to avoid duplication in counts. I collected data on number of broods only during 2008–2010, after which I also recorded chick number and survival data. I followed chicks until they reached 75% adult size or about one-month old, because chick losses are relatively low after this age (De Smet 1987). Thus, one-month old broods represent a good index of juveniles fledged. Grebe adults sometimes temporarily split their brood, each taking some chicks to feed and some adults depart early (Ferguson 1977; De Smet 1983 as cited in Stout and Nuechterlein 2020; G.S.H. pers. obs.), and these behaviours could confound brood size and success data obtained from surveys; thus, extra attention was required to determine true brood number and size. Brood search effort averaged about seven visits/wetland annually 2009–2019 (mean 7.3, range 4–9,  $n = 35$ –54 wetlands).

#### Wetland water level surveys

To look for possible correlations between productivity and wetland water conditions over time, I collected relative water levels measured from a fixed point on permanent stakes hammered into the pond substrate of 15 class IV and V wetlands on or near the block area and averaged the results. These measurements fairly represented local water level change but not all wetlands in this sample contained nesting Red-necked Grebes and no attempt was made to measure water level change on all wetlands occupied by nesting Red-necked Grebes. I developed a wetland scoring system (Table 1, Table S1), primarily for waterfowl (Hammell *et al.* 2021), but applicable

here because the scoring periods are similarly reproductively significant for Red-necked Grebes. The scoring system established criteria for three periods: spring wetland condition (dry to flooded based on pers. obs.), pre-nesting and egg-laying wetland condition (water level drop or rise [cm] from early May to early June), and incubation and brood period wetland condition (water level drop or rise [cm] from early June to mid-July/early August). Red-necked Grebe egg-laying in Manitoba peaks in late May, and 85% of pairs initiate clutches by end of May and peak hatching occurs late June to early July (De Smet 1983 as cited in Stout and Nuechterlein 1999). An annual wetland score was determined for each of the three periods and the sum of these scores represented the wetland score for that year. Generally, the wetter the annual period (defined by higher and/or more stable water levels), the higher the score for that period. I chose these periods because for some waterfowl species (e.g., Lesser Scaup [*Aythya affinis*]; Afton 1984), breeding propensity is positively related to spring wetland condition, where conditions on arrival at the breeding grounds affect the pair's decision to remain and conditions up to the nesting period determine the decision of the female to initiate egg-laying; I propose that grebes may react similarly. Also, nest success for Red-necked Grebes and other grebes (e.g., Horned Grebe) and over-water nesting ducks is positively related to distance from wetland edge (Hammell 1973; Ferguson 1977; Koons 2001; Nuechterlein *et al.* 2003), so Red-necked Grebe productivity may be influenced by water level stability during the egg-laying and incubation period.

#### Data analysis

To calculate local breeding population density and population change over time, I used data from 2011 to 2019 from the primary study area only. I removed data from 2008 to 2010 because of incomplete survey data for those years. The 3–4 pair estimate surveys were averaged, representing the breeding population

**TABLE 1.** Assigned wetland score and scoring parameters describing spring wetland condition and water level change during Red-necked Grebe (*Podiceps grisegena*) pre-nesting–egg-laying and incubation–brood periods, 2009–2019, Erickson, Manitoba.

| Score | Spring wetland condition  | Pre-nesting–egg-laying and incubation–brood periods water level changes (cm) |
|-------|---------------------------|--|
| 5     | Flooded beyond basin      | >10  |
| 4     | Wet grass zone flooded    | 5 to 10  |
| 3     | Sedge* zone flooded       | >0 to 4.9  |
| 2     | Sedge zone dry            | <0 to –4.9   |
| 1     | Bulrush/cattail* zone dry | –5 to –10  |
| 0     | Mudflats showing          | >–10   |

\*Sedge = *Carex* spp.; bulrush/cattail = *Scirpus* spp./*Typha* spp.

for that year. Brood number and pair data (collected 2008–2019) and chick data (collected 2011–2019) on and off the primary study area provided annual productivity estimates: mean broods/breeding pair, mean chicks/breeding pair, and mean chicks/successful pair. For my analysis, pairs recorded during the weekly pair census were considered breeding pairs and the total number of chicks divided by the breeding pair estimate for the same year resulted in the annual number of chicks/breeding pair. Pairs with one or more chicks at 75% adult size were considered successful pairs and the total number of chicks divided by the successful pair estimate for the same year resulted in the annual number of chicks/successful pair. In addition, I calculated weighted means as a comparative metric to account for annual variation in sample size and to make possible a comparison of my results with other studies. I used simple linear regression (data analysis using Microsoft Excel, Redmond, Washington, USA or McDonald 2014 [<https://www.biostathandbook.com/index.html>], earlier in my study) to test the following relationships: (i) breeding population versus year and productivity versus year, (ii) mean broods/breeding pair and chicks/successful pair versus yearly wetland score, and (iii) mean chicks/successful pair versus mean broods/breeding pair.

To examine the effect of the presence of conspecifics and/or wetland size (ha; Acme Planimeter [<https://acme.com/planimeter/>]) on reproduction, I calculated annual broods/breeding pair and chicks/successful pair values for wetlands with one pair (wetland size:  $3.9 \pm 0.5$  ha, range 0.7–8.8,  $n = 22$ ) and for wetlands with more than one pair (~50% of surveyed wetlands;  $8.3 \pm 1.1$  ha, range 1.7–24.2,  $n = 22$ ). Multi-pair wetlands generally are larger than those with single pairs and exposure of nests and chicks to intraspecific aggression and/or wave action on larger wetlands may negatively affect productivity (Nuechterlein *et al.* 2003; C. Paszkowski pers. comm. 13 August 2016; Stout and Nuechterlein 2020). I tested for differences with Wilcoxon signed-rank test for paired data (McDonald 2014) within each year because the distribution of variables was unknown and sample sizes were small. Because data distributions (broods/breeding pair, chicks/successful pair; analyses not shown) indicated that they were similarly shaped and reasonably symmetric, I interpreted results as being tests of differences in mean values. Correlations and differences are considered significant at  $P \leq 0.05$ , and values reported are means  $\pm$  SE.

## Results

The average annual number of Red-necked Grebe pairs in the breeding population for 2011–2019 on the primary study area (22.6 km<sup>2</sup>) was  $60.9 \pm 1.2$  (range

56–66) and showed no trend with year ( $\beta = -0.23$ , SE = 0.48,  $r^2 = 0.032$ ,  $P = 0.60$ ). Average annual pair density was  $2.7 \pm 0.05$  pairs/km<sup>2</sup> (range 2.5–2.9).

Breeding Red-necked Grebes were recorded on 34 (35%) of the 97 class IV and V wetlands on the primary area. The majority of unoccupied class V wetlands were small dugouts. The occupied wetlands were  $6.1 \pm 0.8$  ha (range 0.7–24.2, median 4.6) while the unoccupied wetlands were  $0.7 \pm 0.1$  ha (range 0.01–2.36, median 0.44). Eighty-two percent (28 of 34) of occupied ponds were greater than 2 ha. The wetlands on the primary study area with only one pair for at least one year were  $3.9 \pm 0.5$  ha (range 0.7–8.8,  $n = 22$ ) and those with more than one pair were  $8.3 \pm 1.1$  ha (range 1.7–24.2,  $n = 22$ ); these categories (mean ranks) were significantly different ( $W = 82$ ,  $P < 0.001$ ). Consistency of wetland occupation across years was high (~100%) unless wetlands were altered by landowner draining.

First broods appeared during the last two weeks of June and hatching continued through July. Number of broods/breeding pair (2008–2019), chicks/breeding pair (2011–2019), and chicks/successful pair (2011–2019) are presented in Table 2. Broods/breeding pair ( $\beta = 0.03$ , SE = 0.02,  $r^2 = 0.17$ ,  $P = 0.18$ ,  $n = 12$  years), chicks/breeding pair ( $\beta = -0.10$ , SE = 0.06,  $r^2 = 0.27$ ,  $P = 0.15$ ,  $n = 9$  years), and chicks/successful pair ( $\beta = -0.03$ , SE = 0.04,  $r^2 = 0.08$ ,  $P = 0.46$ ,  $n = 9$  years) were not correlated with year.

Mean broods/breeding pair was positively related to annual wetland score ( $\beta = 0.07$ , SE = 0.02,  $r^2 = 0.49$ ,  $P < 0.02$ ,  $n = 11$  years; Figure 1) but mean chicks/successful pair was not ( $\beta = 0.02$ , SE = 0.06,  $r^2 = 0.01$ ,  $P = 0.80$ ,  $n = 9$  years; Figure 2). Mean chicks/successful pair was positively related to mean broods/breeding pair ( $\beta = 0.99$ , SE = 0.35,  $r^2 = 0.53$ ,  $P = 0.03$ ,  $n = 9$  years; Figure 3).

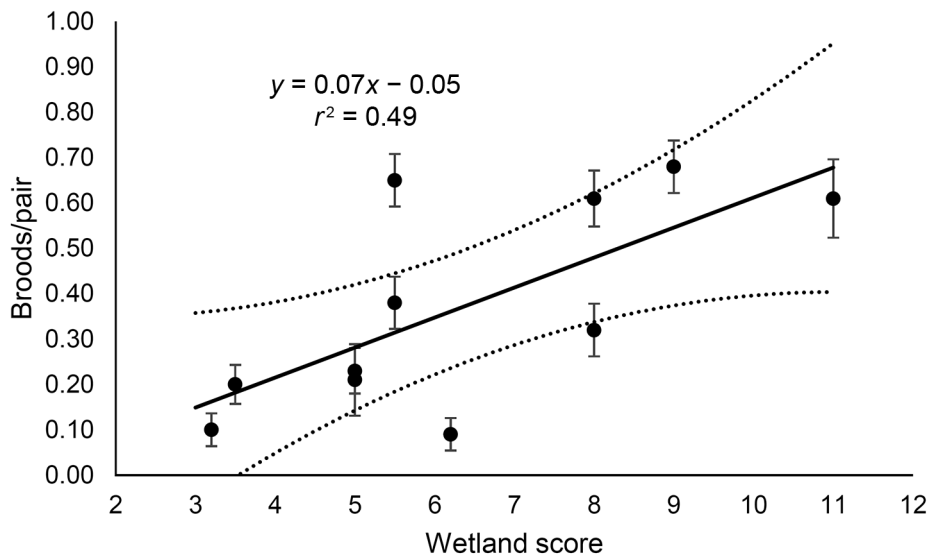
The number of broods/breeding pair on wetlands with a single pair was  $0.36 \pm 0.09$  ( $n = 9$  years and 139 broods; weighted mean:  $0.36 \pm 0.04$ ; Table 3) and for those with multi-pairs was  $0.37 \pm 0.08$  ( $n = 9$  years and 482 broods; weighted mean:  $0.35 \pm 0.02$ ); the difference between the two wetland categories was not significant ( $W = 19$ ,  $n = 9$  years,  $P > 0.2$ ). Similarly, the number of chicks/successful pair on wetlands with a single pair was  $1.59 \pm 0.15$  ( $n = 9$  years and 50 broods; weighted mean:  $1.84 \pm 0.14$ ; Table 3) and for those with multi-pairs was  $1.87 \pm 0.13$  ( $n = 9$  years and 170 broods; weighted mean:  $1.98 \pm 0.08$ ); again the difference was not significant ( $W = 12$ ,  $n = 9$  years,  $P > 0.2$ ). Interestingly, for most years (seven of nine), broods/breeding pair were lower on the largest lake (24.2 ha) than on wetlands with one pair (weighted means:  $0.21 \pm 0.06$ ,  $n = 47$  and  $0.36 \pm 0.04$ ,  $n = 139$ , respectively; Table 3). Similarly, for eight of

**TABLE 2.** Red-necked Grebe (*Podiceps grisegena*) production on 109 surveyed wetlands near Erickson, Manitoba, 2008–2019. “–” indicates no data.

| Year           | No. breeding pairs | No. broods with chicks ~1 month of age (75% of adult size) | Broods/breeding pair  | Total chicks | Mean no. of chicks per breeding pair (SE) | Mean no. of chicks per successful pair (SE) |
|----------------|--------------------|--|-----------------------|--------------|---|---|
| 2008*          | 15                 | 7  | 0.47                  | –            | –   | –   |
| 2009*          | 28                 | 6  | 0.21                  | –            | –   | –   |
| 2010*          | 33                 | 20   | 0.61                  | –            | –   | –   |
| 2011           | 62                 | 38   | 0.61                  | 81           | 1.31 (0.18)                               | 2.13 (0.20)                                 |
| 2012           | 86                 | 17   | 0.20                  | 30           | 0.35 (0.09)                               | 1.76 (0.26)                                 |
| 2013           | 65                 | 21   | 0.32                  | 32           | 0.49 (0.10)                               | 1.52 (0.13)                                 |
| 2014           | 65                 | 44   | 0.68                  | 94           | 1.45 (0.16)                               | 2.14 (0.15)                                 |
| 2015           | 68                 | 44   | 0.65                  | 97           | 1.43 (0.16)                               | 2.20 (0.14)                                 |
| 2016           | 71                 | 27   | 0.38                  | 46           | 0.65 (0.12)                               | 1.70 (0.16)                                 |
| 2017           | 70                 | 16   | 0.23                  | 27           | 0.39 (0.10)                               | 1.69 (0.20)                                 |
| 2018           | 65                 | 6  | 0.09                  | 8            | 0.12 (0.06)                               | 1.33 (0.33)                                 |
| 2019           | 69                 | 7  | 0.10                  | 14           | 0.20 (0.08)                               | 2.00 (0.44)                                 |
| Total          | 697                | 253  |                       | 429          |   |   |
| Mean (SE)      |                    |  | 0.38 (0.06)           |              | 0.71 (0.22)                               | 1.83 (0.10)                                 |
| Weighted mean† |                    |  | 0.36 (0.02, 0–1, 697) |              | 0.69 (0.04, 0–6, 621)                     | 1.95 (0.07, 1–6, 220)                       |

\*Small data set due to reduced size of study area. See text for explanation.

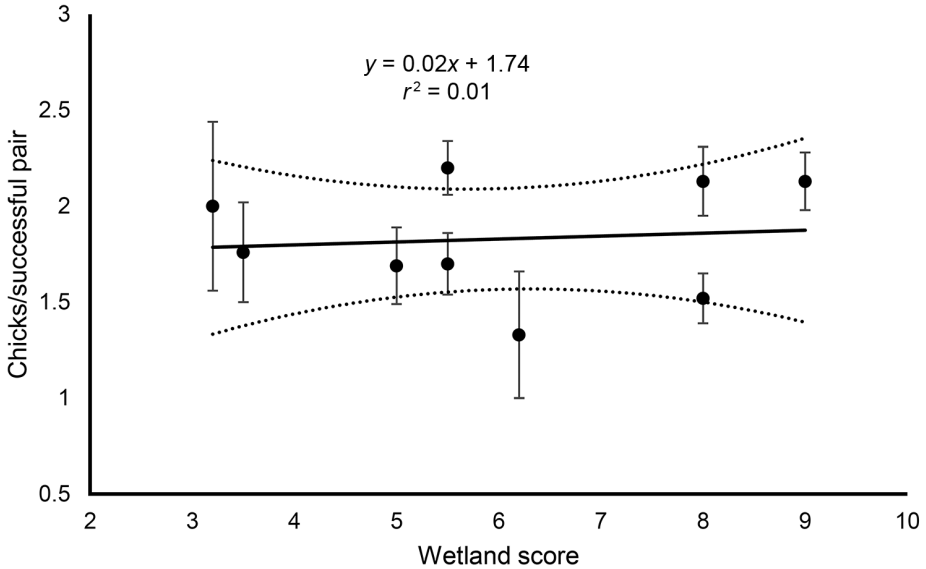
†Weighted mean (SE, range, *n*). Means were weighted by number of years.



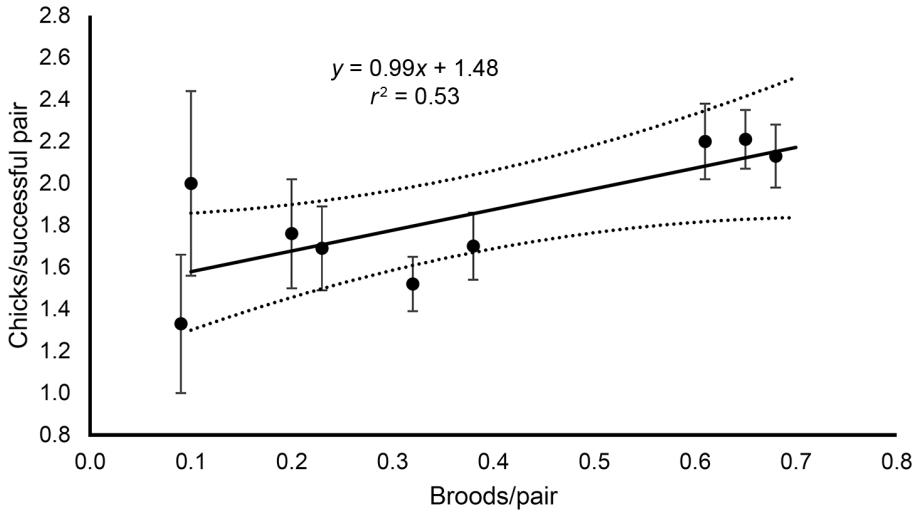
**FIGURE 1.** Linear relationship between Red-necked Grebe (*Podiceps grisegena*) mean broods/breeding pair and wetland score on 109 surveyed wetlands near Erickson, Manitoba, 2009–2019. (Note that ~70 wetlands were surveyed 2009–2010 due to smaller size of study area. See text for explanation.) Wetland score describes relative water conditions during the entire breeding season. Larger wetland scores denote improving wetland condition (see text for description of scoring system). Dotted lines represent a 95% CI (two SE). Bars associated with annual broods/pair means represent one SE.

nine years, annual mean chicks/successful pair ratios were lower on the largest lake than on wetlands with one pair (weighted means:  $1.40 \pm 0.16$ ,  $n = 10$  and

$1.84 \pm 0.14$ ,  $n = 50$ , respectively; Table 3). Annual broods/breeding pair ratios were not significantly different between these categories ( $W = 10$ ,  $n = 9$  years,



**FIGURE 2.** Linear relationship between mean chicks/successful pair for Red-necked Grebe (*Podiceps grisegena*) and wetland score on 109 surveyed wetlands near Erickson, Manitoba, 2011–2019. Wetland score describes relative water conditions during the entire breeding season. Larger wetland scores denote improving wetland condition (see text for description of scoring system). Dotted lines represent a 95% CI (two SE). Bars associated with annual chicks/successful pair means represent one SE.



**FIGURE 3.** Linear relationship between mean chicks/successful pair and mean broods/ breeding pair for Red-necked Grebe (*Podiceps grisegena*) on 109 surveyed wetlands near Erickson, Manitoba, 2011–2019. Dotted lines represent a 95% CI (two SE). Bars associated with annual chicks/successful pair means represent one SE.

$P > 0.1$ ) but annual chicks/successful pair ratios were ( $W = 1, n = 9$  years,  $P < 0.01$ ).

**Discussion**

*Population density and change over time*

Excluding semi-colonial or colonial nesting on large lakes (Wheeler 2001; Nuechterlein *et al.* 2003),

the breeding population densities of greater than 2 pairs/km<sup>2</sup> in my study area in an agriculturally dominated prairie pothole region are some of the highest reported. Populations in boreal habitat in the Northwest Territories were 0.1–3.2 birds/km<sup>2</sup> or 1.6 pairs/km<sup>2</sup> (Fournier and Hines 1998; D. Kay pers. comm. in Fournier and Hines 1998) and in Alaska, were

**TABLE 3.** Red-necked Grebe (*Podiceps grisegena*) annual broods/ breeding pair and chicks/successful pair for wetlands with one pair ( $n = 12\text{--}22$ ) and the largest wetland (24.2 ha) in the dataset near Erickson, Manitoba, 2011–2019.

| Year      | Wetlands with one pair                 |  | Largest wetland: > one pair            |  |
|-----------|--|--|--|--|
|           | Broods/breeding pair<br>(no. of pairs) | Chicks/successful pair<br>(no. of pairs) | Broods/breeding pair<br>(no. of pairs) | Chicks/successful pair<br>(no. of pairs) |
| 2011      | 0.81 (16)                              | 2.38 (13)                                | 0.60 (5)                               | 1.67 (3)                                 |
| 2012      | 0.25 (12)                              | 2.00 (3)                                 | 0.25 (8)                               | 1.50 (2)                                 |
| 2013      | 0.20 (15)                              | 1.33 (3)                                 | 0.67 (3)                               | 1.00 (2)                                 |
| 2014      | 0.67 (15)                              | 1.70 (10)                                | 0.25 (4)                               | 1.00 (1)                                 |
| 2015      | 0.63 (16)                              | 1.80 (10)                                | 0.20 (5)                               | 2.00 (1)                                 |
| 2016      | 0.42 (12)                              | 1.80 (5)                                 | 0.17 (6)                               | 1.00 (1)                                 |
| 2017      | 0.14 (22)                              | 1.33 (3)                                 | 0.00 (6)                               | 0.00 (0)                                 |
| 2018      | 0.07 (14)                              | 1.00 (1)                                 | 0.00 (5)                               | 0.00 (0)                                 |
| 2019      | 0.06 (17)                              | 1.00 (2)                                 | 0.00 (5)                               | 0.00 (0)                                 |
| Mean (SE) | 0.36 (0.09)                            | 1.59 (0.15)                              | 0.24 (0.08)                            | 0.91 (0.25)                              |

0.02–0.14 birds/km<sup>2</sup> (Stout and Nuechterlein 2020). Mean long-term (1991–2018) density at Yellowknife, Northwest Territories, is 0.84 pairs/km<sup>2</sup> (Environment and Climate Change Canada unpubl. data). Corrigan (2007) reported Red-necked Grebe densities during 1989–2007 in east-central Alberta were 0.06–0.66 birds/km<sup>2</sup>. Such high densities near Erickson suggest that the pothole habitat in southern Manitoba is now very attractive to breeding pairs and provide a sharp contrast to very low breeding densities in the 1970s (0.0–0.1 pairs/km<sup>2</sup>, Hammell 2017).

Why then, have breeding populations changed so dramatically in southern Manitoba? De Smet (2018) speculated that increases may be partly explained by wet conditions in the region over the past two decades, but numbers had begun increasing marginally from the early 1970s to the early 1980s (J. Austin unpubl. data). Also, high levels of organochlorine pesticides in grebe eggs were reported for many studies in the past (see De Smet 1987 for summary) and were thought to be negatively affecting many aspects of reproduction for grebes and other birds. Levels of these chemicals have declined since the 1970s (Forsyth *et al.* 1994) and Hammell (2017) speculated that this reduction may have led to increased productivity and consequently, increased juvenile recruitment and immigration into parkland habitat. But these hypotheses have not been tested and reasons for population increases remain unclear.

At Erickson, breeding pairs occupied all available wetlands of sufficient size and depth (semi-permanent and permanent ponds greater than 2 ha), similar to populations in other southern breeding areas (Stout and Nuechterlein 2020). However, in southwestern Manitoba (Hammell 2017; this study) some Red-necked Grebes occupied wetlands (not dugouts) less

than 1 ha, consistent with Fournier and Hines' (1998) observations in the Northwest Territories. Such occupancy patterns suggest some flexibility in choice of breeding wetland, perhaps when suitable habitat configuration (wetland density) exists (Fournier and Hines 1998; Hammell 2017). During my study, breeding population size was stable and pair numbers on many ponds were usually the same or differed by only one or two pairs from year to year. In addition, broods/breeding pair and chicks/breeding and /successful pair, although annually variable, exhibited no significant trend over the study period, consistent with a population experiencing little long-term change. If the Erickson Red-necked Grebe breeding population exhibited the classic logistic S-shaped growth curve associated with species pioneering a novel environment (Odum 1959), then, collectively, these results suggest that the population may have moved beyond the rapid growth stage and probably has reached carrying capacity. This is most likely due to constraints of intraspecific aggression and territoriality although other unknown covariates could be additional factors. The permanent and semi-permanent breeding wetlands of Red-necked Grebes can be altered by periods of drought (Rogers 1964) resulting in reduced area and periphery and ultimately lower breeding populations (Corrigan 2007). Climate change projections for the prairie and parkland area suggest drier summers, potentially producing rapidly falling water levels and reduced Red-necked Grebe productivity (Sorenson *et al.* 1998; Sauchyn *et al.* 2020).

#### *Comparative productivity estimates*

The mean number of chicks/breeding pair I documented was lower than that reported from all but one other study area in Canada, however, the mean number of chicks/successful pair was similar or

higher than all but one other study (Table 4). Therefore, in the agriculturally-dominated landscape of southern Manitoba, productivity (juveniles recruited/breeding pair) seems to be lower than in most other areas, including in forested habitat in southern Manitoba (De Smet 1987). Wetlands surrounded by forest may provide advantages not seen in areas experiencing greater human disturbance (e.g., protection of nests from wave action on forested wetlands, De Smet 1987). However, measures of reproductive success exhibit high interannual variability due to variation in environmental conditions and longer-term studies provide more accuracy in truly assessing reproductive rates.

A comparison of my results with those published from the longer-term study of boreal wetlands near Yellowknife conducted by Fournier and Hines (1998) might provide greater insight into differing reproductive rates. My results (Table 2) for average broods/breeding pair were lower (0.38 versus 0.72) and exhibited a wider range (0.09–0.68) than those reported for the Northwest Territories (0.51–0.85). Possible (but unsubstantiated) causes may include differing predator community and more stable wetland water levels in the boreal ecozone than in the parkland ecozone. Raccoons are a serious predator of over-water waterfowl and grebe nests in southern Manitoba (Hammell 1973; Ferguson 1977; De Smet 1987) but are not part of the predator community at Yellowknife (C. Wood pers. comm. 8 January 2020). In addition, wetlands in northern latitudes do not experience as dramatic a change in water levels as seen in lower latitudes because of short, cool summers with near equal annual precipitation and evapotranspiration (Woo and Winter 1993). Falling wetland water levels presumably allow mammalian predators easier access to over-water nests (see below). Consequently, Red-necked Grebe nests in boreal wetlands with more stable water levels and lacking Raccoons

may be less vulnerable to mammalian predation than those in the parkland area, resulting in less overall nest predation. Similarly, Fournier and Hines (1999) found that mammalian predation on Horned Grebe nests at the same Yellowknife study area was lower than that reported in Manitoba by Ferguson (1977). Accordingly, boreal Red-necked Grebes may be more productive than those in the parkland because broods/breeding pair and chicks/breeding pair in all studies across the Canadian prairie provinces were lower than for boreal breeders at Yellowknife.

#### *Productivity and wetland water levels*

Red-necked Grebe productivity (broods/breeding pair) was positively related to annual wetland score, a proxy for water level that sums an initial score for the spring and changes in water levels for the pre-nesting–egg laying period and incubation–brood periods. This is not surprising because Red-necked Grebe nest exclusively over-water and width of emergent vegetation band and distance to dryland edge may be critical to success. Nuechterlein *et al.* (2003) working with Red-necked Grebes in central Minnesota, USA, found that experimental artificial nests located farther from adjacent shores were more successful than those located directly adjacent to shore concluding that nests that were located farther from land or over deeper water presumably were safer from terrestrial predators such as Raccoons. Similarly, Frederick and Collopy (1989), found that as little as 5–10 cm of water can greatly deter mammalian predators on shorebird nests. Hammell (1973) for Lesser Scaup and Ferguson (1977) for Horned Grebe found mean distance of successful overwater nests to pond edge was greater than that of unsuccessful nests suggesting that falling wetland water levels would place more nests closer to shoreline and potential predators. Collectively, these studies highlight the importance of wet, stable water level years to overwater nesting avian species.

**TABLE 4.** Measures of reproductive success (weighted mean  $\pm$  SD, range, *n*) of Red-necked Grebe (*Podiceps grisegena*) in Canada. Means are weighted by number of years of study.

| Study area                         | Source                               | Chicks/breeding pair     | Chicks/successful pair   |
|------------------------------------|--------------------------------------|--------------------------|--------------------------|
| Erickson, Manitoba                 | My study (nine years)                | 0.7 $\pm$ 1.1 (0–6, 621) | 2.0 $\pm$ 1.0 (1–6, 220) |
| Turtle Mountains, Manitoba         | De Smet (1983; two years)*           | 0.9 $\pm$ 1.3 (0–6, 104) | 2.1 $\pm$ 1.1 (1–6, 43)  |
| Astotin Lake, Alberta              | Kevan (1970; one year)*              | 1.1 $\pm$ 1.2 (0–5, 89)  | 1.8 $\pm$ 1.0 (1–5, 52)  |
| Alberta potholes                   | Riske (1976; seven years)*           | 1.1 $\pm$ 0.1 (63)       | 1.6 $\pm$ 0.1 (41)       |
| Pine Lake, Alberta                 | Riske (1976; seven years)*           | 0.4 $\pm$ 0.1 (267)      | 1.4 $\pm$ 0.1 (51)       |
| Duck Lake, British Columbia        | Ohanjanian (1986; three years)*†     | No data                  | 1.7 $\pm$ 0.5 (1–2, 34)  |
| Yellowknife, Northwest Territories | Fournier and Hines (1998; 10 years)* | 1.4†                     | 2.0†                     |

\*Site-specific estimates as cited in Stout and Nuechterlein (2020).

†10-year average.

The number of chicks/successful pair (brood size) was not positively related to annual wetland score despite brood size being positively associated to broods/breeding pair which did show a positive trend with increasing annual wetland score. This lack of positive correlation between brood size and wetland score is surprising and unexplained. Ferguson and Sealy (1983), working 20 km south of my study area, proposed that water level was an important determinant of Horned Grebe nest success through its controlling influence on the distribution of emergent vegetation. Wet years usually produce wide peripheral bands of lush, new, emergent growth coupled with previous year's growth (e.g., *Scirpus* spp. and *Typha* spp.), areas where adult Red-necked Grebes with chicks on-back or older juveniles may be able to rest or hide, presumably safer from mammalian or aerial predators. During dry years, both adults and chicks are forced to abandon dry emergent beds for more exposed wetland centres (G.S.H. pers. obs.).

#### *Productivity and the presence of conspecifics*

Intraspecific aggression can impart both costs and benefits that potentially could affect productivity. By defending a territory, adults may gain additional resources for eggs and/or themselves leading to increased number of young, but costs may include eggs lost from unattended nests and injuries obtained in competitive interactions (De Smet 1987; Garner 1991). Increased expenditures of energy and time by adults during aggressive encounters could result in less time providing for young. I was unable to detect reproductive differences (broods/breeding pair and chicks/successful pair) between wetlands with only one pair and those with more than one pair, suggesting that pairs on multi-pair wetlands may be as productive as single pairs. De Smet (1987) found that depredation and organochlorine pollutants were responsible for most nesting losses; those from territoriality were minimal. Nuechterlein *et al.* (2003) found no effect of crowding on nest success among semi-colonial and solitary nesting Red-necked Grebes on a large (2537 ha) shallow lake in Minnesota, USA. However, semi-colonial pairs nested on floating cattail-mat islands, which may have lowered the risk of mammalian depredation (Nuechterlein *et al.* 2003). Klatt *et al.* (2004) concluded that the ability of Red-necked Grebes to change behaviour in response to social circumstances allows them to breed successfully in a variety of situations from strongly solitary to loosely colonial aggregations. At Erickson, solitary pairs nested around the wetland periphery; similarly, grebes on multi-pair wetlands nest around the periphery usually at distances exceeding 75 m (G.S.H. pers. obs.). Presumably such spacing provides adequate resources for adults and

young with minimal disturbance from neighbouring pairs.

Nest destruction from wave action is commonly reported as a reason for nest failure in studies on large lakes (Wheeler 2001; Nuechterlein *et al.* 2003; Riske 1976 as cited in Stout and Nuechterlein 2020), but wave-related losses were few in sheltered small to medium-sized lakes in wooded habitat in southern Manitoba (De Smet 1987). How wetland size covaries with intraspecific aggression in Erickson area wetlands to affect production is unknown but few wetlands used by Red-necked Grebes are entirely surrounded by trees and all are windswept to some degree. My dataset comprised relatively small wetlands (all but one  $\leq 15$  ha), and on the largest lake (24 ha), broods/breeding pair and chicks/successful pair for most years were lower than those on smaller single-pair wetlands suggesting that wetlands larger than those involved in this study might have lowered productivity. C. Paszkowski (pers. comm. 13 August 2016) observed that, despite success at the egg laying, nesting, and even hatching phase, survival of young to fledging can be quite low on larger, but still shallow, lakes in central Alberta. Larger, shallow lakes (over 25 ha and up to several hundred ha in size) occur in the Erickson area, representing  $\sim 10\%$  of permanent wetlands (G.S.H. pers. obs.), and therefore, further analysis using a dataset that included larger wetlands than surveyed here might provide additional insight into Red-necked Grebe productivity in southern Manitoba.

#### *Conclusions*

My study provides a comparative point of reference for the Red-necked Grebe population breeding in agriculturally-dominated habitat in southern Manitoba and provides additional data to aid the development of region-specific integrated population models (Zhao *et al.* 2020). Such modelling might identify drivers of population growth rate and help draft appropriate conservation strategies. My results introduce one potential driver of productivity in parkland pothole habitat, notably, wetland score as a proxy for water level.

To my knowledge, Red-necked Grebe breeding densities in southwestern Manitoba are the highest reported for solitary-nesting pairs in North America, and the breeding population appears to be stable during the study period, perhaps having reached carrying capacity. My productivity results suggest that chicks/breeding pair is lower but chicks/successful pair is similar or greater than reported in most other studies. Pairs breeding on larger wetlands along with other conspecifics appear to be as productive as solitary pairs on smaller, single-pair wetlands, but the range and diversity of wetlands included in my study was

limited. Prolonged drought or permanent changes in climate leading to warmer, drier summers on the prairies and parklands could reduce breeding populations. Periodic review of the population and productivity status of Red-necked Grebes in areas with long-term datasets (e.g., southwestern Manitoba, Yellowknife study area) would provide added information beyond that obtained from the BBS, enabling better interpretation of trend data.

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#### SUPPLEMENTARY MATERIAL:

**TABLE S1.** Assigned scores for spring wetland condition, pre-nesting–egg-laying, and incubation–brood periods for Red-necked Grebe (*Podiceps grisegena*), near Erickson, Manitoba, 2009–2019.