Arch. Geflügelk. 2002, **66** (3), 124–132, ISSN 0003-9098. © Verlag Eugen Ulmer GmbH & Co., Stuttgart

Reproductivity and raising of Greater Rhea (*Rhea americana*) and Lesser Rhea (*Pterocnemia pennata*) – a review

Reproduktion und Aufzucht von Großen Nandus (*Rhea americana*) und Kleinen Nandus (*Pterocnemia pennata*) – eine Übersicht

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Manuskript eingegangen am 20. März 2001, angenommen am 6. Oktober 2001

Introduction

The Greater or Common Rhea (*Rhea americana*) and the Lesser or Darwin's Rhea (*Pterocnemia pennata*) are flightless birds native from South America, that have conservation and economic importance. Free-ranging populations of these ratites have been detrimentally affected by human activities (BUCHER and NORES, 1988; CARMAN, 1988; MARTELLA et al., 2000). On the other hand, during the 1990s the farming of ratites, including rheas, experimented a boom-and-bust process in USA, Canada and some European countries (CHAPMAN and BASS, 1994; NARA, 1994a; DEEMING and ANGEL, 1996; CARBAJO et al., 1997; CASTELLÓ, 1998a; DEY, 1998; GILLESPIE and SCHUPP, 1998). More recently, this activity has increased as an agricultural business and as a means for human subsistence and recreation in several countries within the natural range of the species (mainly in Argentina, Uruguay, and Brazil) (GIANONI, 1996; NAVARRO, 1999; AUCRIÑA, 2000).

There are two common schemes for rearing adult rheas: the captive or intensive condition that is implemented by most zoos and farms, and the semi captive or semi intensive condition that is being adopted by an increasing number of producers, mainly in South America (this latter practice is also commonly used for farming Ostriches in South Africa). The captive alternative uses breeder pens $\leq 1200\ m^2$ housing 1 or 2 males and 3 to 4 females, which are mainly fed with processed bagged feed. The semi captive or semi extensive condition comprises large paddocks ≥ 1 ha, where breeding flocks -up to approximately 15 birds per ha- freely mate and graze in a pasture such as alfalfa (*Medicago sativa*), and receive a comparatively smaller quantity of processed feed. The first management practice generally contemplates only artificial incubation, whereas under the second, the producer can rely either on artificial or on natural incubation, or use a combination of both.

Understanding demography of rheas is necessary to design appropriate management strategies for this near-threatened species and to help decision-making at commercial farms and captive breeding programs. Comprehensive studies on reproductive parameters of wild Greater Rheas are scarce, and we are not aware of any study of this type on Lesser Rheas. For the former species, they exist only for two populations of the subspecies present in Argentina (*R. a. albescens*), in Buenos Aires province (BRUNING, 1974; FERNÁNDEZ and REBOREDA, 1998, 2000), and one population of other subespecies (*R. a. intermedia* or *R. a. americana*) in southeastern Brazil (CODENOTTI, 1995, 1997). Additionally, some isolated parameters of these and related species are directly or indirectly provided in short works, and reports, from zoos and farms (reviewed in this paper). However, most of the latter studies are based on performance of few and comparatively small groups of breeders and true replications are almost nonexistent.

The aim of this work is to summarize all the current knowledge on productivity in rheas and to compare the breeding performance of these species versus other related ones, under different management schemes. We also suggest management recommendations for the captive breeding and conservation of rheas.

Behavioural and ecological factors affecting demography

The Greater Rhea exhibits a peculiar breeding system that plays a relevant role in its demography. The mating system of the species has been described as a combination of harem polygyny and sequential polyandry (BRUNING, 1974; ORING, 1982), or a promiscuity produced by a mixture of both previously mentioned systems and simultaneous polyandry (HANDFORD and MARES, 1985; MARTELLA et al., 1994, 1998). The male has a dominant role in reproduction. He performs courtship displays (RAIKOW, 1969), constructs the nest scrape in the ground (where multiple females lay eggs) and assumes the full incubation of the eggs, which hatch almost synchronously after 5 to 6 weeks. Chicks are precocial and able to feed themselves, but they remain associated for several months with an adult male. He guides them to food, and provides warmth, cover and protection against predators. Besides rearing their own flock of chicks, males adopt chicks (BRUNING, 1974; MARTELLA et al., 1994; CODENOTTI and ALVAREZ, 1998; LÁBAQUE et al., 1999). Although the Lesser Rhea has been studied in less detail than the Greater Rhea, evidences (BALMFORD, 1992; SARASQUETA, 1995, 1997; NAVARRO et al., pers obs.) suggest that breeding systems of both species are similar.

In wild Greater Rheas, a substantial and variable proportion of males do not produce chicks each year (BRUNING, 1974; FERNÁNDEZ and REBOREDA, 1998). Nest desertion is common and some males do not even attempt to construct a nest, which may be related to the age of the

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male or its social status (MARTELLA et al., 1998). Variations in the proportion of incubating males modify the growth rate of Greater Rhea populations through a change in birth rate. Therefore, an estimation of the fraction of incubating males within the population should be required in demographic studies of rheas.

Egg laying

The breeding season of the Greater Rhea is restricted from early-spring to mid-summer. The laying season of wild populations in southeastern Brazil (CODENOTTI, 1997) and Buenos Aires province (FERNÁNDEZ and REBOREDA, 1998) overlap with egg laying in Córdoba (NAVARRO and MARTELLA, 1998; NAVARRO et al., unpubl. data). The laying season of the Lesser Rhea in farms of the Argentine Patagonia extends from mid-winter to late-spring (SARASQUETA, 1997; NAVARRO et al., 2000).

Slight to moderate variations in the date of start and the length of the breeding season, and important differences in breeding performances of rheas have been observed, even among populations located comparatively close to each other. The photoperiod (influenced by latitude) may be responsible of differences at larger geographic scales, while climate (temperature and rainfall) can contribute to these fluctuations and to variations among years. On the other hand, possible reasons for local differences within a given year could be: (1) higher quality or quantity of food sources (natural and supplementary); (2) superior quality of nesting and brooding sites (less prone to flooding or predation); (3) better quality (higher genetic diversity and lesser relatedness) or composition (sex ratio) of the breeding stock; (4) lower population density; or (5) a combination of these factors.

Breeding and rearing

Clutch size of Greater Rheas is the largest among ratites in the wild (median = 25 eggs, excluding the outlier data of 120 eggs), followed by the Lesser Rhea (20 eggs), Emu (20 eggs), Ostrich (19 eggs), Cassowaries (7 eggs) (Table 1), and Kiwis (2 eggs; DEL HOYO et al., 1992). Throughout the breeding season, a Greater Rhea female can lay a median of 30 eggs, which is similar to that of the Emu, larger than the Cassowaries (7 eggs), and less than the Ostrich (40 eggs) (Table 2). On the other hand, Lesser Rhea females produce a lower number of eggs per season (median = 19 eggs) than Greater Rheas and the other two farmed ratite species, being only higher than the non-commercially bred species (Cassowaries and Kiwis).

Although both Rhea species do not show the highest egg production per female among ratites, the comparatively high hatching success of their eggs (medians: Lesser Rhea 67 %, Greater Rhea 58 %, Ostrich 50 %, Emu 48 % and Cassowaries 37 %) (Table 3), counterbalances in part for the differences in number of hatchlings produced per female.

Survival of young chicks and juveniles of ratites are lower than in poultry. Both rhea species show the lowest medians of rearing success (nr. of chicks alive in autumn/nr. of hatched eggs) among ratites: Greater Rhea 45 %, Lesser Rhea 52 %, Ostrich 60.5 %, Emu 86 %, and Cassowaries 83 % -only one data-) (Table 4). These figures, combined with respective hatching success, lead to rheas having a comparatively low median breeding success (nr. of chicks alive in autumn/nr. of egg laid) with respect to other ratites: Greater Rhea 20 %, Lesser Rhea 23 %, Ostrich 35 %, Emu 30 %, and Cassowaries < 52 % (Table 5). Also, median survival of Greater Rhea chicks (data available only for this species) from hatching to the subsequent spring is slightly lower (63 %) than in the Ostrich (69 %) (Table 6).

Finally, if one estimates the number of surviving chicks in autumn produced per female (median number of egg per female times breeding success/100) under captive conditions, the Ostrich shows to be the most productive ratite (14 chicks per female), followed by the Emu (11 chicks), Cassowaries (9 chicks), Greater Rhea (8 chicks), and Lesser Rhea (4 chicks).

Reproductive performance of rheas under different rearing conditions

Under captive (farms and zoos) and semi captive conditions, both rhea species have clutch sizes (median: Greater

Table 1. Clutch size of the Greater Rhea (*Rhea americana*), the Lesser Rhea (*Pterocnemia pennata*), and other ratites.
Gelegegröße des Großen Nandus (Rhea americana), des kleinen Nandus (Pterocnemia pennata) und anderer Flachbrustvögel

Species	Clutch size	Management	Hemisphere	Location	Reference/s
Greater Rhea	15–120	Wild populations	South	Argentina	review by CARMAN (1988)
(Rhea americana)	20–30	Wild populations	South	Brazil	*fide* SICK (1985)
	20–35	Semi captive population	South	Córdoba, Argentina	NAVARRO and MARTELLA (1998)
	21	Wild population	South	Córdoba, Argentina	MARTELLA and NAVARRO, unpubl. data
	22	Wild population	South	Río Grande do Sul, Brazil	calculated from CODENOTTI (1995)
	25	Wild population	South	Buenos Aires, Argentina	calculated from FERNÁNDEZ and REBOREDA (1995)
	27	Wild populations	South	Buenos Aires, Argentina	BRUNING (1974)
	30	Wild population	South	Río Negro, Argentina	SARASQUETA (2000)
	40	Wild populations	South	Brazil	*fide* SANTOS (1952)
Lesser Rhea	19, 20	Wild population	South	Río Negro, Argentina	SARASQUETA (1995), (2000)
(Pterocnemia pennata)	20	Wild population	South	Río Negro, Argentina	BELLIS et al. (2000)
	26	Farm	South	Río Negro, Argentina	GIAI (1943)
Ostrich	5–11	Wild population	South	n/a	*fide* ULLREY and ALLEN (1996)
(Struthio camelus)	14–22	Wild population	South	Tsavo East Nt.Pk., Kenya	LEUTHOLD (1977)
	15–36	Wild population	South	Tsavo West Nt.Pk., Kenya	BERTRAM (1992)
	16–23–34	Wild population	South	Tsavo East Nt.Pk., Kenya	*fide* LEUTHOLD (1977)
	ca. 36	Wild population	South	Nairobi Nt.Pk., Kenya	*fide* LEUTHOLD (1977)
Emu	5–20	Wild population	South	Western Australia	DAVIES (1976)
(Dromaius novaehollandiae)	30	Zoo	North	Manitoba, Canada	BOWTHORPE and VOSS (1968)
Cassowaries	3–8	Wild population	South	Queensland, Australia	CROME (1976)
(Cassuarius spp.)	7	Zoo	North	Colorado, USA	BIRCHARD et al. (1982)

fide = according to

Table 2. Eggs per female of the Greater Rhea (*Rhea americana*), the Lesser Rhea (Pterocnemia pennata), and other ratites.
Eizahl je Henne beim Großen Nandu (Rhea americana), kleinen Nandu (Pterocnemia pennata) und anderen Flachbrustvögeln

Species	Eggs per female	Management	Hemisphere	Location	Reference/s
Greater Rhea	7	Zoo	North	Warsaw, Poland	Calculated from KACZMAREK and POHORECKA (1965)
(Rhea	10–18	Wild populations	South	Brazil	fide SICK (1985)
americana)	11–24–35	Semi captive population	South	Córdoba, Argentina	NAVARRO and MARTELLA (1998); NAVARRO et al., unpubl. data
	13	Zoo	North	Manitoba, Canada	BOWTHORPE and VOSS (1968)
	14	Zoo	South	Río de Janeiro, Brazil	BRITO (1949)
	15–60	Farms	North	North America	*fide* BEAVERS (1992)
	21	Zoo	North	Great Witchingham, UK	WAYRE (1966)
	21–49	Zoo	North	Karnataka State, India	GOWDA (1961)
	25	Farm	North	Wales, UK	H. MACFIE, *in litt.*
	27	Farm	South	Río Negro, Argentina	SARASQUETA (1997)
	30–40	Wild populations	South	Brazil	*fide* DANI (1993)
	40	Farm	South	Brazil	*fide* SANTOS (1952)
	40–55	Farms	South	Brazil	*fide* GIANONI (1996)
	40–60	Farms	North	USA	*fide* STEWART (1992, 1994)
	>40	Zoo; Farms	North; n/a	Missouri, USA; n/a	FLIEG (1973); fide BLAKE (1996); DEY (1998)
	42	Zoo	North	Texas, USA	calculated from BROWN and KIMBELL (1972)
	44	Farms	South	Central Argentina	LÁBAQUE et al., unpubl. data
Lesser Rhea	6–12	Zoo	North	Illinois, USA	KRUCZEC (1968)
(Pterocnemia	10–30	Farms	South	North Patagonia, Argentina	NAVARRO et al. (2000)
pennata)	14–17	Farm	South	Río Negro, Argentina	SARASQUETA (1995)
	19–53	Farms	South	Río Negro, Argentina	NAVARRO et al. (1998b)
	25–48	Farms	South	Río Negro, Argentina	NAVARRO et al. (1999a)
	27	Wild population	South	Southern Chile	BALMFORD (1992)
Ostrich	15–31	Farm	South	Eastern Australia	MORE (1996a)
(Struthio	18	Farms	North	Louisiana, USA	GILLESPIE et al. (1996)
camelus)	20–40	Farms	North	USA	KOCAN and CRAWFORD (1999)
	20–70	Farms	n/a	n/a	*fide* GURRI (1997)
	22–50, 92	Farm	North	France	*fide* GURRI (1996)
	32	Farm	South	Western Cape, South Africa	calculated from BLOOD et al. (1998)
	35–55	Farms	North	USA	*fide* JEFFEREY (no date -a-)
	39	Farms	North	France	*fide* CASTELLÓ (1998a)
	40–60	Farms	North	North America; Europe	*fide* BEAVERS (1992); *fide* ALVAREZ DE LA PUENTE (1996)
	40–75	Farms	n/a	n/a	*fide* CASTELLÓ (1997)
	>40	Farms	n/a	n/a	*fide* BLAKE (1996)
	50	Farms	n/a	n/a	*fide* CASTELLÓ (1998b)
	60–70	Farms	n/a	n/a	*fide* MARÍN and CERVÑO (1996)
	<60	Farms	n/a	n/a	*fide* ULLREY and ALLEN (1996)
	64	Zoo	North	Missouri, USA	FLIEG (1973)
	68	Farm	North	Texas, USA	*fide* CHISHOLM TRAIL OSTRICH Farm (1992)
Emu	20–35	Farms	n/a	n/a	*fide* CARBAJÓ and CASTELLÓ (1997)
(Dromaius	23	Farms	North	Louisiana, USA	GILLESPIE et al. (1996)
novaehollan	30–33	Zoo	North	Manitoba, Canada	BOWTHORPE and VOSS (1968)
-diae)	>30	Farms	North; n/a	USA; n/a	*fide* JEFFEREY (no date -b-); *fide* BLAKE (1996)
	<50	Farms	North	North America	*fide* BEAVERS (1992)
Cassowaries	3–5	Zoo	North	Scotland, UK	FISHER (1968)
(Cassuarius spp.)	3–8	Wild populations	South	Queensland, Australia	CROME (1976)
	7–14	Zoo	North	Colorado, USA	SCHMITT (1983); BIRCHARD et al. (1982)

Rhea = 28 eggs; Lesser Rhea = 26 eggs, only one data available) slightly higher than those recorded in the wild (Greater Rhea median = 25 eggs; Lesser Rhea = 20 eggs) (Table 1). The number of eggs produced per Greater Rhea females at farms and zoos (median = 40 eggs) is higher than that of Lesser Rheas (18 eggs). Greater Rheas also show a higher egg production per female under captive conditions than in semi captivity (median = 24 eggs) (Table 2). The hatching success of Greater Rheas is also higher under captive condition (median = 60 %) than in semi captivity (45 %) and in the wild (30 %), whereas Lesser Rheas show an opposite trend (captivity = 51 %; wild = 60 %) (Table 3).

Extra foods given in a more regular basis and predator exclusion are probably the responsible factors of these differences that lead to higher productivity of Greater Rheas under captivity. The lower figures showed by Lesser Rheas at farms are probably the result of quantitatively and qualitatively inadequate dietary schemes observed in several cases in the Argentine Patagonia (NAVARRO et al., pers. obs.).

Causes of egg loss and chick mortality

Heavy rains, nest disturbation and predation of eggs and chicks seem to be important direct and indirect sources of nest desertion and mortality (FERNÁNDEZ and REBOREDA, 1998; NAVARRO et al., unpubl. data). Also, diseases threaten rhea survival and eventually affect egg production and hatching success. Disease deserves further study, because its effect could be important under some circumstances. Chicks seem to be much more prone to death due to disease-related problems than adults (CHANG REISSIG et al., in press).

High population densities promote excessive encounters and fights among males. This could, in turn, interfere with social interactions, courtship behavior, nesting, incubation, and rearing and survival of chicks (MARTELLA et al., unpubl. data).

Poaching of eggs, chicks or adults for food should not be underrated as a cause of disturbance under normal circumstances. Preliminary research with radio-tracked rheas showed that poaching may be of even

Table 3. Hatching success (nr. of hatched eggs / total nr. of eggs) of the Greater Rhea *(Rhea americana)*, the Lesser Rhea *(Pterocnemia pennata)*, and other ratites.
Schlupfrate (Anzahl geschlüpfter Küken/Gesamtanzahl eingelegter Eier) des Großen Nandus (Rhea americana), des kleinen Nandus (Pterocnemia pennata) und anderer Flachbrustvögel

Species	Hatching success (%)	Management	Hemisphere	Location	Reference/s
Greater Rhea *(Rhea americana)*	10–35	Zoo	South	Río de Janeiro, Brazil	BRITO (1949)
	11–34	Semi captive population	South	Córdoba, Argentina	NAVARRO et al. (1997); NAVARRO and MARTELLA (1998)
	17	Wild population	South	Buenos Aires, Argentina	FERNÁNDEZ and REBOREDA (1998)
	28–43	Zoo	North	Karnataka State, India	GOWDA (1961)
	30	Wild population	South	Buenos Aires, Argentina	calculated from FERNÁNDEZ and REBOREDA (1995)
	46	Zoo	North	Manitoba, Canada	BOWTHORPE and VOSS (1968)
	50	Zoo	North	Great Witchingham, UK	calculated from WAYRE (1966)
	54–66–70	Farm	North	Wales, UK	H. MACFIE, *in litt.*
	55–60	Semi captive population	South	Córdoba, Argentina	NAVARRO (1999); NAVARRO et al. (1999b)
	58	Zoo	North	New York, USA	BRUNING (1973)
	60	Zoo	North	Texas, USA	calculated from BROWN and KIMBELL (1972)
	60	Farm	South	San Luis, Argentina	VIGNOLO et al. (1999)
	65	Wild population	South	Buenos Aires, Argentina	BRUNING (1974)
	67	Farms	North	USA	NARA (1994b)
	67	Zoo	North	Warsow, Poland	KACZMAREK and POHORECKA (1965)
	69	Farms	South	Central Argentina	LÁBAQUE et al., unpubl. data
	71	Farm	South	Sao Paulo, Brazil	PASCHOAL and MAGNANI (1988)
	75	Farm	North	UK	BUTTER (1919)
	96	Ranching from wild population	South	Río Negro, Argentina	SARASQUETA (2000)
Lesser Rhea *(Pterocnemia pennata)*	14	Zoo	North	USA	RISSER and TOWNE (1977)
	19–46–78	Farms	South	North Patagonia, Argentina	NAVARRO et al. (2000)
	23–41–70	Farms	South	Río Negro, Argentina	NAVARRO et al.(1999a)
	38	Zoo	North	California, USA	calculated from KUEHLER and GOOD (1990)
	44–73	Wild population	South	Río Negro, Argentina	SARASQUETA (1995)
	46–77	Zoo	North	Illinois, USA	KRUCZEK (1968)
	50, 75–100	Ranching from wild populations	South	Río Negro, Argentina	SARASQUETA (2000)
	51–80	Farms	South	Río Negro, Argentina	NAVARRO et al. (1998b)
	60	Wild populations	South	Río Negro, Argentina	calculated from BELLIS et al. (2000)
	67	Zoo	North	New York, USA	BRUNING (1973)
	78–80	Farm	South	Río Negro, Argentina	*fide* SARASQUETA (1995)
Ostrich *(Struthio camelus)*	3	Farm	South	Zimbabwe	FOGGIN and HONYWILL (1992)
	24–28	Farm	North	UK	DEEMING (1996a, 1996b)
	28	Farms	North	Louisiana, USA	GILLESPIE et al. (1996)
	29	Zoo	North	California, USA	calculated from KUEHLER and GOOD (1990)
	33	Wild	South	Nairobi Nt. Pk., Kenya	*fide* ULLREY and ALLEN (1996)
	35–48	Farm	North	UK	DEEMING (1995a, 1995b, 1996b)
	38–60	Farm	North	UK	DEEMING et al. (1993a)
	39–50	Farm	South	Western Cape, South Africa	CLOETE et al. (1998)
	41–44	Farm	North	Israel	AR and GEFEN (1998)
	43	Farm	South	Eastern Australia	MORE (1996b)
	47–63	Farm	South	Western Cape, South Africa	DAVIS et al. (1998)
	49	Farm	North	UK	DEEMING and AYRES (1994)
	<50	Zoo	North	Missouri, USA	calculated from FLIEG (1973)
	50	Farms	North	Europe	*fide* ALVAREZ DE LA PUENTE (1996)
	50	Farms	South	South Africa	SMITH et al. (1995) *fide* DEEMING and AR (1999)
	50–59	Farm	South	Western Cape, South Africa	BRAND et al. (1998)
	57	Farms	n/a	n/a	calculated from MARÍN and CERVIÑO (1996)
	58	Farm	South	Australia	MORE (1997)
	58	Farm	North	Israel	ANON (1999) *fide* DEEMING and AR (1999)
	58–77	Farms	n/a	n/a	CASTELLÓ (1997)
	62	Farms	South	South Africa	VAN SCHALKWYK et al. (1996), VAN SCHALKWYK and CLOETE (1999)
	65	Wild populations	South	Tsavo West Nt.Pk., Kenya	BERTRAM (1992)
	70	Farms	North	USA	*fide* JEFFEREY, no date -a-
	70–80	Farms	South	South Africa	VERWOERD et al. (1998) *fide* DEEMING and AR (1999)
	72	Farms	n/a	n/a	*fide* CASTELLÓ (1998b)
Emu *(Dromaius novaehollandiae)*	33	Zoo	North	California, USA	calculated from KUEHLER and GOOD (1990)
	43–45	Zoo	North	Manitoba, Canada	BOWTHORPE and VOSS (1968)
	45	Farm	South	Western Australia	BEUTEL et al. (1983)
	48–75	Farms	n/a	n/a	*fide* CARBAJÓ and CASTELLÓ (1997)
	50–80	Farms	North	USA	*fide* JEFFEREY (no date -b-)
	57	Farms	North	Louisiana, USA	GILLESPIE et al. (1996)
Cassowaries *(Cassuarius spp.)*	0–33-100	Zoo	North	Scotland, UK	FISHER (1968)
	7	Zoo	North	Colorado, USA	BIRCHARD et al. (1982)
	>41	Zoo	North	Colorado, USA	SCHMITT (1983)

greater importance than habitat modification, in threatening the persistence of rheas in central Argentina (BELLIS et al., 1999). One potential solution to poaching is to give viable economic alternatives to rural people, such as programs for the sustainable use of wild populations. When local residents have a financial interest in preserving wildlife, poaching may be eradicated (CAMPFIRE ASSOCIATION, 1990).

Table 4. Rearing success (nr. alive in autumn/nr. of hatched eggs) of the Greater Rhea *(Rhea americana)*, the Lesser Rhea *(Pterocnemia pennata)*, and other ratites.
Überlebensrate der Küken (Anzahl lebender Küken im August/Anzahl geschlüpfter Küken) beim Großen Nandu (Rhea americana), beim kleinen Nandu (Pterocnemia pennata) und bei anderen Flachbrustvögeln

Species	Rearing success (%)	Management	Hemisphere	Location	Reference/s
Greater Rhea	3–64	Farm	n/a	n/a	CHAPMAN and BASS (1994)
(Rhea	4–31	Farm	North	Wales, UK	H. MACFIE, *in litt.*
americana)	23–50	Semi captive population	South	Córdoba, Argentina	NAVARRO et al., unpubl. data; NAVARRO et al. (1997)
	26	Wild population	South	Buenos Aires, Argentina	FERNÁNDEZ and REBOREDA (1998)
	40	Zoo	North	Warsaw, Poland	KACZMAREK and POHORECKA (1965)
	50	Wild population	South	Córdoba, Argentina	MARTELLA and NAVARRO, unpubl. data
	58–60	Semi captive population	South	Córdoba, Argentina	NAVARRO (1999); NAVARRO et al. (1999b)
	80	Zoo	South	Río de Janeiro, Brazil	BRITO (1949)
Lesser Rhea	5–18–40–78	Farms	South	North Patagonia, Argentina	NAVARRO et al. (2000)
(Pterocnemia	17	Zoo	North	Illinois, USA	calculated from KRUCZEC (1968)
pennata)	51–83	Farms	South	Río Negro, Argentina	NAVARRO et al. (1999a)
	52–89	Farms	South	Río Negro, Argentina	NAVARRO et al. (1998b)
	61	Zoo	North	New York, USA	BRUNING (1973)
Ostrich	24–85	Farms	n/a	n/a	calculated, *fide* CASTELLÓ (1997)
(Struthio	38	Farms	North	France	*fide* CASTELLÓ (1998a)
camelus)	<41	Wild population	South	Tsavo East Nt.Pk., Kenya	calculated from LEUTHOLD (1977)
	60	Farms	North	Louisiana, USA	GILLESPIE et al. (1996)
	61	Farm	South	Eastern Australia	MORE (1999c)
	67–78	Farm	North	UK	DEEMING et al. (1993b)
Emu	70–86	Zoo	North	Manitoba, Canada	BOWTHORPE and VOSS (1968)
Dromaius	85	Farms	North	Louisiana, USA	GILLESPIE et al. (1996)
novaehollandiae)	88–93	Farms	n/a	n/a	*fide* CARBAJO and CASTELLÓ (1997)
Cassowaries *(Cassuarius spp.)*	83	Zoo	North	Colorado, USA	BIRCHARD et al. (1982)

Table 5. Breeding success (nr. alive in autumn/nr. of eggs laid) of the Greater Rhea *(Rhea americana)*, the Lesser Rhea *(Pterocnemia pennata)*, and other ratites.
Zuchterfolg (Anzahl lebender Küken im August/Anzahl gelegter Eier) beim Großen Nandu (Rhea americana), beim kleinen Nandu (Pterocnemia pennata) und bei anderen Flachbrustvögeln

Species	Breeding success (%)	Management	Hemisphere	Location	Reference/s
Greater Rhea	3–20	Semi captive population	South	Córdoba, Argentina	NAVARRO et al., unpubl. data
(Rhea americana)	<42	Farm	North	Wales, UK	H. MACFIE, *in litt.*
Lesser Rhea	8	Zoo	North	Illinois, USA	KRUCZEC (1968)
(Pterocnemia pennata)	38	Farms	South	North Patagonia, Argentina	NAVARRO et al. (1998b), Navarro (1999)
Ostrich	17	Farms	North	Louisiana, USA	GILLESPIE et al. (1996)
(Struthio camelus)	35–65	Farms	n/a	n/a	*fide* CASTELLÓ (1997)
Emu	23–36	Zoo	North	Manitoba, Canada	BOWTHORPE and VOSS (1968)
(Dromaius novaehollandiae)	15–50	Farm	n/a	n/a	calculated, *fide* CARBAJO and CASTELLÓ (1997)
Cassowaries *(Cassuarius spp.)*	<52	Zoo	North	Colorado, USA	calculated from SCHMITT (1983)

Table 6. Survival from hatching to the subsequent spring, of the Greater Rhea *(Rhea americana)* and the Ostrich *(Struthio camelus)*.
Überlebensrate der Küken vom Schlupf bis zum nächsten Frühjahr beim Großen Nandu (Rhea americana) und beim Strauß (Struthio camelus)

Species	Survival (%)	Management	Hemisphere	Location	Reference/s
Greater Rhea	25	Wild populations	South	Buenos Aires, Argentina	FERNÁNDEZ and REBOREDA (1998)
(Rhea americana)	40	Semi captive population	South	Córdoba, Argentina	NAVARRO et al., unpubl. data
	63	Wild populations	South	Río Grande do Sul, Brazil	calculated from CODENOTTI (1995)
	<79	Farm	North	Wales, UK	H. MACFIE, *in litt.*
	<85	Farm	n/a	n/a	calculated from Dey (1998)
Ostrich *(Struthio camelus)*	56–81	Farms	n/a	n/a	*fide* CASTELLÓ (1997)

Adult survival

Contrary to that observed in young, adult rheas have very high survival rates. Based on a gross adult survival estimate obtained in semi captive populations of Greater Rheas in Córdoba (Argentina) (NAVARRO et al., unpubl. data), and using a maximum-likelihood equation: $MLS = 1/(-Ln(S_a))$; being S_a a constant survival estimate for adults (SEBER, 1973), the average adult life span of rheas will be 13 years. However, this value could be significantly increased if some complementary management measures were taken to reduce or avoid fortuitous adult mortality (see below).

Generality of the actual productivity of ratites

The lowest figures observed in reproductive parameters of ratites correspond mostly to early works, when information about the breeding and rearing of species of this group was completely lacking. Other papers reported cases in which productivity was affected by different causes of loss. On the other hand, the largest figures for all ratite species are systematically observed in general, ornithological, or commercially oriented literature. Most of these cases lack field data and/or rely either on anecdotal data, or on population values that are not currently achieved by the species. In other cases, specific sources of the figures they mention can not be easily checked, because they are cited in an ambiguous way, or not cited at all.

Reproductive parameters of all ratites reported in the majority of scientific works conducted at commercial and experimental farms and zoos, actually show to be more moderate than those claimed in general or commercial literature. Therefore, the higher limits of the intervals reported in the latter kind of works should be recognized as exaggerated and misleading, as they are seldom, if ever, attained in reality. In fact, an actual challenge that faces the ratite industry is to gain knowledge of efficient production practices to improve the performance at the different stages of the production cycle (GILLESPIE et al., 1996; GILLESPIE and SCHUPP, 1998; VAN ZYL, 1998). Particularly fertility, hatching, and raising of ratites generally show figures that are far lower than in poultry industry (VAN ZYL, 1998; DEEMING and AR, 1999).

Currently, research from which to derive the best management practices for rhea production is still scarce. As a consequence, this activity is now in a similar phase to that described by GILLESPIE and SCHUPP (1998) for the ratite industry in the United States. This phase is characterized by producers experimenting with a wide array of input mixes (in which some of them do not necessarily hold for each particular situation), and thus achieving highly variable productivity and efficiency.

Management recommendations

The better reproductive performance observed in other farmed ratites that are closely related to rheas, suggest that if some management measures are implemented the performance of rheas reared under captivity and semi-captivity can be substantially improved. Moreover, a point could be reached in which the semi captive alternative may show a better cost/effectiveness ratio than keeping adult breeders in pens.

The following management considerations can contribute for achieving higher productivity of rheas under semi-captive conditions: (1) In a given paddock, the density of adult males should be maintained below 3 males per ha; (2) Taking into account the promiscuous mating system of the species and the disproportional contribution of males to parental care, in ranching schemes where only natural incubation is feasible, an even sex ratio will generally enable the maximum egg production by females (i.e., the longest laying period). On the other hand, a female biased sex ratio is preferable when population size is low (e.g., small scale operations or at the starting phase of a farm) or in those captive-breeding operations where appropriate artificial incubators are available; (3) Control of potential predators (e.g., dogs, cats, foxes, opossums, lizards, snakes, armadillos and raptors), or their exclusion by means of adequate wire fences and electric fences, is important for enhancing survival of rheas of all ages; (4) Periodic search and removal of small foreign objects (e.g., nails, wires, and other sharp objects) will reduce mortality due to ingestion of harmful matter; (5) Watering troughs that are accessible to chicks should be shallow. The same applies to feeders, except if their design allows the evacuation of water; (6) Poles, faucets and other immobile objects should be placed, arranged or painted to make them easy to view from a distance (even at night) or, at least, improbable to hit; (7) Provision of supplementary food (e.g., ratite or chicken pellets) could enhance productivity and survival; (8) Periodic removal of feces for early detection and treatment against parasites will decrease chick mortality; (9) Areas used for nesting should be provided with good drainage. However, in areas where the abandonment of clutches is high, due to nest flooding or desertion of males, brood manipulation and artificial incubation would be an effective measure; and (10) The release of artificially produced chicks into areas that have males with their own broods is also advisable, to reduce the efforts and costs of chick rearing either in ranches or captive breeding programs (see also LÁBAQUE et al., 1999).

We stress that the recommendations listed above are based on the best knowledge we have about rheas and can be, therefore, improved as the information on these and related species increases. However, they are valuable for the present development of site-specific management and conservation strategies for the Greater Rhea and the Lesser Rhea, and some maybe extrapolated to related species. Our recommendations could be useful for programs that implement sustainable use, management in established reserves or large ranches, captive or semi-captive breeding, and reintroduction, addition, or translocation of rheas.

Summary

The Greater Rhea (*Rhea americana*) and the Lesser Rhea (*Pterocnemia pennata*) are ratites that have conservation and economic relevance. The two most common schemes for rearing adult rheas are the captive or intensive condition in pens (used by most zoos and farms), and the semi captive or semi intensive condition in large breeding paddocks. Understanding demography of rheas is necessary to design management strategies for these species and to help decision-making at farms and captive breeding programs. The median total number of eggs produced per season by Greater Rhea females under captive condition (40 eggs) is higher than that of Lesser Rheas (18 eggs). Greater Rheas also show a higher egg production under captivity than in semi captivity (24 eggs). The hatching success of Greater Rheas is higher in captivity (median = 60 %) than in semi captivity (45 %), or in the wild (30 %), whereas Lesser Rheas show the opposite trend (captivity = 51 %, wild = 60 %). Finally, the estimated number of surviving chicks in autumn produced per female rheas are lower than that of other ratites: Ostrich = 14 chicks; Emu = 11 chicks; Cassowaries = 9 chicks; Greater Rheas = 8 chicks; and Lesser Rheas = 4 chicks. Reproductive parameters of all ratites reported in most scientific works show to be more moderate than those commonly claimed in general or commercial literature. Although both rhea species show a comparatively

low productivity, incorporating specific management practices suggested in this work into the different rhea production schemes can substantially improve egg laying, hatchability, and survival of chicks and adults.

Keywords

Ratite, *Rhea*, *Pterocnemia*, ostrich, emu, reproduction, farming environment, management

Zusammenfassung

Reproduktion und Aufzucht von Großen Nandus *(Rhea americana)* und Kleinen Nandus *(Pterocnemia pennata)* – eine Übersicht

Der Große Nandu (*Rhea americana*) und der kleine Nandu (*Pterocnemia pennata*) gehören zu den Flachbrustvögeln (Ratitae) und sind sowohl für den Naturschutz als auch aus wirtschaftlichen Überlegungen von Bedeutung. Am häufigsten werden erwachsene Nandus in Gefangenschaft oder unter intensiven Produktionsbedingungen in Gehegen (in erster Linie in Zoos und auf Farmen) sowie unter Gefangenschafts-ähnlichen und semi-intensiven Bedingungen in großen Zuchtkoppeln gehalten. Zum Verständnis der Bevölkerungsstatistik der Nandus ist es wichtig, Management-Strategien für diese Spezies zu entwickeln und zur Entscheidungsfindung der Farmen und der Zuchtprogramme für gefangene Tiere beizutragen.

Bei Haltung unter Gefangenschaftsbedingungen ist der Median der Gesamteizahl je Saison für weibliche Große Nandus höher (40 Eier) als für Kleine Nandus (18 Eier). Große Nandus legen in Gefangenschaft mehr Eier als unter Gefangenschafts-ähnlichen Bedingungen (24 Eier). Die Schlupfrate ist bei Großen Nandus in der Gefangenschaft (Median = 60 %) höher als unter Gefangenschafts-ähnlichen Bedingungen (54 %) oder in der Wildnis (30 %). Demgegenüber ist bei Kleinen Nandus der umgekehrte Trend zu beobachten (Gefangenschaft 51 %, Wildnis 60 %). Die geschätzte Anzahl der überlebenden Küken im August, die je Henne geschlüpft waren, lag für die Nandus niedriger als für die anderen Ratitae: Strauß = 14, Emu = 11, Kasuare = 9, Großer Nandu = 8, Kleiner Nandu = 4. Die in den meisten wissenschaftlichen Arbeiten berichteten Reproduktionsparameter aller Ratitae sind geringer als in allgemeiner und kommerzieller Literatur angegeben. Obwohl beide Nandu-Spezies eine vergleichsweise niedrige Reproduktionsleistung aufweisen, wird davon ausgegangen, dass durch die Anwendung spezifischer Managementmaßnahmen, wie dies in der vorliegenden Arbeit für verschiedene Produktionsverfahren für Nandus aufgezeigt wurde, die Legerate, die Schlupfrate und die Überlebensfähigkeit der Küken und der erwachsenen Tiere signifikant verbessert werden kann.

Stichworte

Ratitae, *Rhea*, *Pterocnemia*, Nandu, Strauß, Emu, Reproduktion, Farmhaltung, Management

Acknowledgements

We are indebted to S. R. Beissinger and two anonymous referees for critically reading an earlier version of the manuscript, and to G. Giacone for checking the English. Grants from the Consejo de Investigaciones Científicas y Tecnológicas de la Provincia de Córdoba, and the Secretaría de Ciencia y Técnica de la Universidad Nacional de Córdoba supported the study. Research and manuscript preparation were mostly carried out during the stay of JLN and MBM in the University of California at Berkeley (USA), hosted by S. R. Beissinger, which was supported with a fellowship from FOMEC to JLN and from FONCYT to MBM.

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