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Growth and sex effects on the expression of syndecan-4 and glypican-1 in turkey myogenic satellite cell populations

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Abstract The adult skeletal muscle stem cells, satellite cells, are responsible for skeletal muscle growth and regeneration. Satellite cells represent a heterogeneous cell population that differentially express cell surface markers. The membrane-associated heparan sulfate proteoglycans, syndecan-4, and glypican-1, are differentially expressed by satellite cells during the proliferation and differentiation stages of satellite cells. However, how the population of syndecan-4- or glypican-1-positive satellite cells changes during proliferation and differentiation, and how sex and muscle growth potential affect the expression of these genes is unknown. Differences in the amount of satellite cells positive for syndecan-4 or glypican-1 would affect the process of proliferation and differentiation which would impact both muscle mass accretion and the regeneration of muscle. In the current study, the percentage of satellite cells positive for syndecan-4 or glypican-1 from male and female turkeys from a Randombred Control Line 2 and a line (F) selected for increased 16-week body weight were measured during proliferation and differentiation. Growth selection altered the population of syndecan-4- and glypican-1-positive satellite cells and there were sex differences in the percentage of syndecan-4- and glypican-1-positive satellite cells. This study provides new information on dynamic changes in syndecan-4- and glypican-1-positive satellite cells showing that they are differentially expressed during myogenesis and growth selection and sex affects their expression.

Keywords Glypican-1 · Heterogeneity · Muscle · Satellite cell · Syndecan-4

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Introduction

Satellite cells were first discovered by Mauro [1] and were named due to their peripheral location in skeletal muscle fibers: between the muscle fiber membrane and the basal lamina. Satellite cells are undifferentiated mononuclear myogenic precursor cells. They have the ability to self-renew, maintain, repair, and increase muscle fiber size by proliferation, differentiation, and fusion with existing muscle fibers [2, 3]. Satellite cells are normally quiescent in adults [4, 5]. However, when skeletal muscle tissue is injured or heavily used, the satellite cells become active and re-enter the cell cycle [6, 7]. Satellite cells proliferate, fuse with damaged myofibers, or form new myofibers through a process similar to fetal muscle formation [8].

The Pax3+/Pax7+ muscle progenitor cells from the dermomyotome give rise to satellite cells of the trunk and limbs [9–12]. Satellite cells of extraocular and branchial arch muscles arise from the head mesoderm [13, 14]. Thus, muscle satellite cells are a heterogeneous population of cells [15]. Satellite cells from different muscles will differentially express the same gene. For example, satellite cells from the diaphragm have a higher level of Pax3 expression compared to satellite cells in the limb muscles [16].

Satellite cells from the same muscle and even the same fiber can also express different markers. For example, not all satellite cells express M-cadherin, CD34, or Myf5 [3, 17]. Furthermore, satellite cells isolated from the same muscle can vary in growth potential and responsiveness to growth factor stimuli [18, 19].

Satellite cells are primarily active during the growth phase of animals and at the end of the growth phase, the number of satellite cells decreases to less than 5 % of total myofiber nuclei and become largely quiescent [20]. Quiescent satellite cells express the transcription factor Pax7 [21], cell adhesion protein M-cadherin [22], myogenic regulatory factor Myf5 [17, 23, 24], and saliomucin CD34 [17]. Cell membrane proteins syndecan-3 and syndecan-4 [25], lysenin [26], and caveolin 1 [27] are also quiescent satellite cell markers. Satellite cells re-enter the cell cycle in response to various stresses including, but not limited to, damage from injury or exercise. When activated, satellite cells begin to express muscle-specific proteins such as desmin and myogenic transcription factors, such as MyoD, myogenin [28–30], and MRF4 [31, 32]. Myf5, Pax7, M-cadherin, and CD34 are also expressed in activated satellite cells. Some of the markers differentially expressed by satellite cells are cell membrane proteins. These cell membrane proteins can be used to separate satellite cell populations with a fluorescence-activated cell sorter.

Syndecan-4 and glypican-1 are cell membrane heparan sulfate proteoglycans. These heparan sulfate proteoglycans are differentially expressed by satellite cells during proliferation and differentiation, and regulate satellite cell growth and development in different ways [33–39]. In the current study, the percentage of syndecan-4- or glypican-1-positive cells in turkey pectoralis major muscle satellite cells was measured during proliferation and differentiation of male and female satellite cells, and the effect of growth selection on the syndecan-4 and glypican-1 populations of satellite cells was determined. This study is the first to investigate changes in syndecan-4- or glypican-1-positive satellite cells during turkey skeletal muscle satellite cell proliferation and differentiation in male and female cells, and the effect of growth selection using fluorescence-activated cell sorter separation as a means to measure syndecan-4 and glypican-1 expressing satellite cells.

Materials and methods

Satellite cell culture

Satellite cells isolated from the pectoralis major muscle of 7-week-old male and female randombred control line 2 (RBC2) and F-line turkeys were used [40]. The RBC2-line is representative of a 1967 turkey and has been maintained at The Ohio State University, Ohio Agricultural Research and Development Center Poultry Research Unit without conscious selection for any trait. From the RBC2-line, a turkey line was selected for only increased 16-week body weight (F-line: [41]), and has significantly higher pectoralis muscle weight than the RBC2-line [42]. The F-line body weight and pectoralis major muscle weight at 16-week of age were 10,950 and 1,546 g, whereas the RBC2-line body weight and pectoralis major weight were 6,490 and 848 g, respectively. As shown previously by Velleman et al. [40] growth selection has affected the proliferation and differentiation properties of the F-line satellite cells. Satellite cells were plated in gelatin-coated 6-well cell culture plates (Greiner Bio-One) at the density of 36,000 cells/well in plating medium [Dulbecco's modified eagle medium (DMEM; Sigma-Aldrich) containing 10 % chicken serum (Gemini), 5 % horse serum (Gemini), 1 % antibiotic/antimycotic (Gemini), and 0.1 % gentamicin (Gemini)] and incubated in a 37.5 °C 5 % CO_2/95 % air incubator. After a 24-h attachment, the plating medium was changed to feeding medium [McCoy's 5A medium (Sigma-Aldrich) containing 10 % chicken serum, 5 % horse serum, 1 % antibiotic/antimycotic, and 0.1 % gentamicin]. Feeding medium was changed daily until 96 h proliferation. Differentiation was induced when cells reached 60 % confluency by changing the feeding medium to fusion medium [DMEM containing 3 % horse serum, 1 % antibiotic/antimycotic, 0.01 mg/mL porcine gelatin (Sigma-Aldrich), 0.1 % gentamicin, and 1.0 mg/mL bovine serum albumin (Sigma-Aldrich)]. The fusion medium was changed every 24 h until 72 h of differentiation.

Guava expressplus assay

At 48, 72, and 96 h of proliferation, and 24, 48, and 72 h of differentiation, cells were rinsed twice with PBS (pH 7.08), scraped off the plates, and transferred to a 1.5 mL tube. The cells were collected by centrifugation at $800\times g$ for 10 min at room temperature. After removing the supernatant, the cells were washed twice by resuspending the pellet in 1.5 mL PBS. The cell concentration was then adjusted to 5×10^7 cells/mL. Two hundred and fifty microliters of each sample was added to 0.5 μL of either goat anti-syndecan-4 (Santa Cruz, 1:500) or goat anti-glypican-1 (Santa Cruz, 1:500) antibodies and incubated overnight at 4 °C. After being washed three times with PBS, cells were incubated with donkey anti-goat Alexa Fluor-488 (Invitrogen, 1:500) antibody at room temperature for 30 min. Cells were then washed three times with PBS and analyzed on a Guava EasyCyte system (Millipore) following the manufacturer's Guava ExpressPlus assay protocol. In brief, the Guava EasyCyte system detects fluorescence from the secondary antibody. The total number of cells positive for

syndecan-4 or glypican-1 was determined which was then used to calculate the percentage of syndecan-4- or glypican-1-positive cells. Only the percentage of cells expressing either syndecan-4 or glypican-1 was measured.

Statistical analysis

All experiments were repeated independently at least three times. For each experiment, three cell culture wells were prepared for each treatment group (male or female; F- or RBC2-line satellite cells), and the data from each culture well were used to calculate a mean and the standard error of the mean (SEM). Data are graphed as the mean ± SEM. The SAS PROC GLM (SAS Institute Inc., Cary, NC) was used for statistical analyses. Differences among means were detected using the Fisher's least significance method. Differences among means in each experiment were evaluated using an ANOVA and detected using Fisher's least significant difference. Two-sided P values of $P < 0.05$ were considered statistically significant.

Results

Syndecan-4- and glypican-1-positive cells in RBC2 and F-line male and female turkey satellite cells

In RBC2-line male turkey satellite cells, the percentage of glypican-1-positive cells was higher than that of syndecan-4 during both proliferation and differentiation stages (Fig. 1a). During proliferation, the percentage of both syndecan-4- and glypican-1-positive cells declined from 16 % and 23 % to 0 % at 96 h of proliferation. The number increased during differentiation and peaked at 48 h of differentiation for glypican-1 (34 %) and 72 h of differentiation for syndecan-4 (11 %). In F-line male turkey satellite cells, the percentage of glypican-1-positive cells was higher than that of syndecan-4 during proliferation and lower during differentiation (Fig. 1b). At 72 h of differentiation the percent of syndecan-4- and glypican-1-positive cells were 20 and 26 %, respectively. The percentage decreased to 2.61 and 3.28 % at 24 h of differentiation. The amount of glypican-1-positive cells increased from 24 to 72 h of

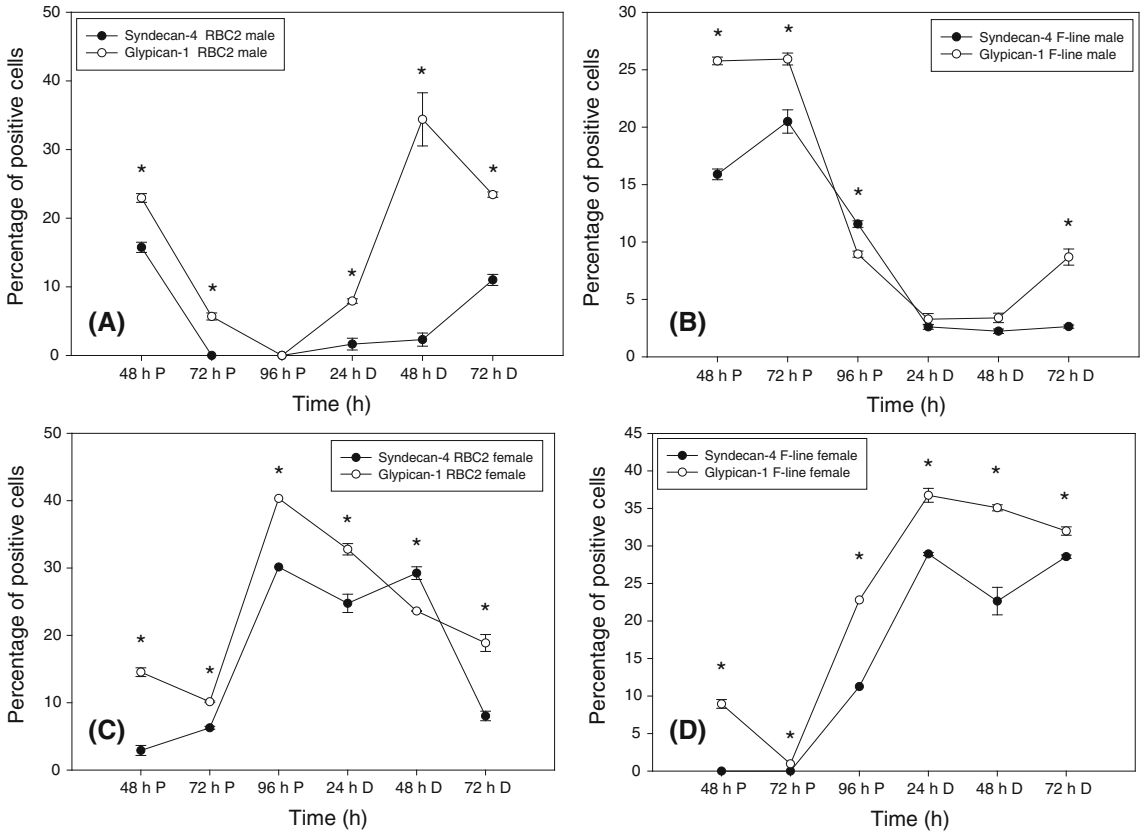

Fig. 1 Percentage of syndecan-4- or glypican-1-positive cells in randombred control line 2 (RBC2) and 16-wk body weight selected F-line male and female turkey satellite cells. **a** Percentage of syndecan-4- and glypican-1-positive cells in RBC2-line male turkey satellite cells from 48 h of proliferation (P) to 72 h of differentiation (D), **b** percentage of syndecan-4- and glypican-1-positive cells in F-line male turkey satellite cells from 48 h P to 72 h D, **c** percentage of syndecan-4- and glypican-1-positive cells in RBC2-line female turkey satellite cells from 48 h P to 72 h D, and **d** percentage of syndecan-4- and glypican-1-positive cells in F-line female turkey satellite cells from 48 h P to 72 h D. *Bars* represent the standard error of the mean. *Indicates a significant difference at $P < 0.05$

differentiation, whereas the syndecan-4-positive cell percentage remained similar throughout the remainder of differentiation.

In RBC2 female turkey satellite cells, the percentage of glypican-1-positive cells was 15 % at 48 h of proliferation, decreased to 10 % at 72 h of proliferation, and then peaked at 96 h of proliferation at 40 % (Fig. 1c). During differentiation, the percentage of glypican-1-positive female RBC2 satellite cells decreased to 19 % at 72 h of differentiation. The syndecan-4-positive cells in the RBC2 female turkey satellite cells increased during proliferation from 3 to 30 % (Fig. 1c). During differentiation, the percent decreased to 25 % at 24 h of differentiation and by 72 h of differentiation it was 8 %.

In contrast to the RBC2 female line satellite cells, the F-line female satellite cells had increased syndecan-4 and glypican-1 expression during differentiation (Fig. 1d). The glypican-1-positive cells were 9 % at 48 h of proliferation, decreased to less than 1 % at 72 h of proliferation, and peaked at 37 % at 24 h of differentiation. In terms of syndecan-4, there were no detectable positive cells at both 48 and 72 h of proliferation. The percentage of satellite cells expressing syndecan-4 increased to 29 % at 24 h of differentiation, and remained high throughout differentiation with 29 % of the cells being positive for syndecan-4 at 72 h of differentiation.

Comparison of syndecan-4 and glypican-1 expression profiles during proliferation and differentiation in RBC2 and F-line female and male turkey satellite cells

The percentage of syndecan-4-positive cells in RBC2 male turkey satellite cells was lower than in F-line male turkey satellite cells during both proliferation and differentiation except at 72 h of differentiation (Fig. 2a). At 48 h of proliferation, the percentage of syndecan-4-positive cells in the RBC2 and F-line male turkey satellite cells was ~15 % and by 48 h of differentiation had declined to 2 % in both lines. In F-line male turkey satellite cells, the percentage of syndecan-4-positive cells peaked at 72 h of proliferation, decreased until 24 h of differentiation, and

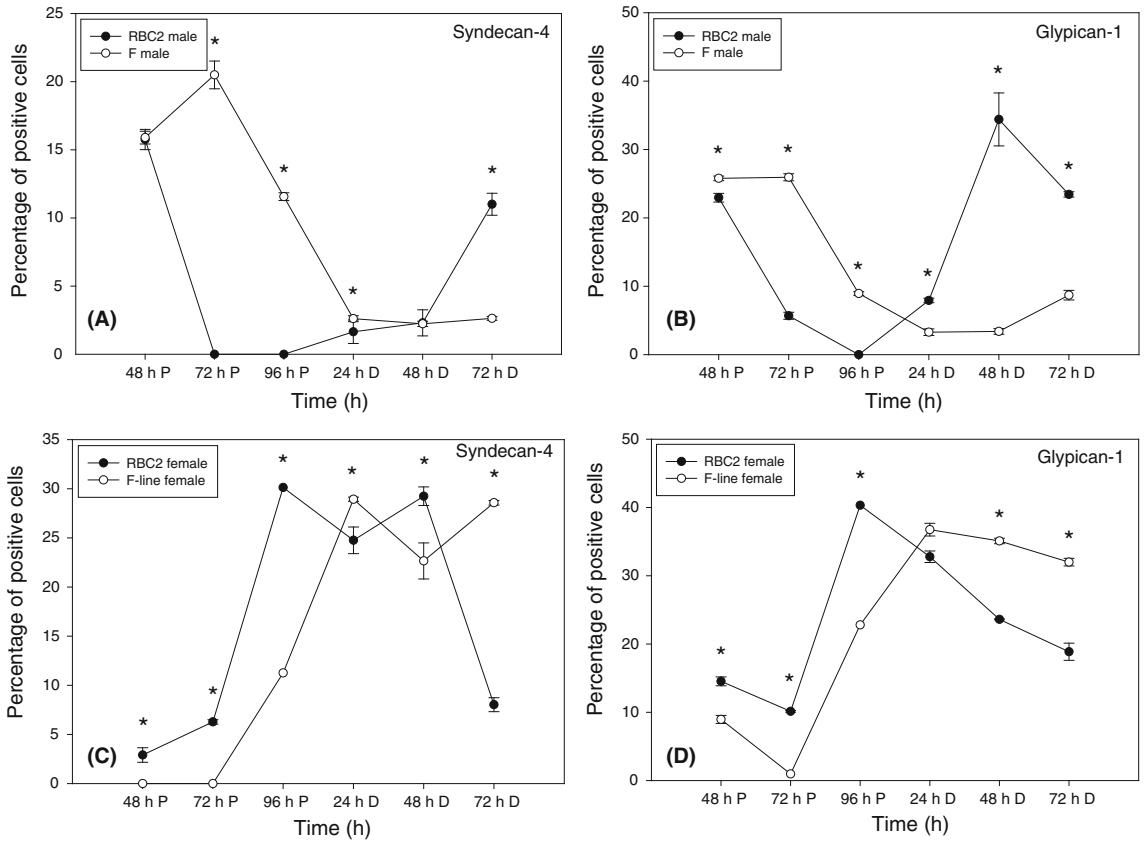

Fig. 2 Comparison of the percentage of syndecan-4- or glypican-1-positive cells in randombred control line 2 (RBC2) and 16-week body weight selected F-line male and female turkey satellite cells. **a** Percentage of syndecan-4-positive cells in RBC2 and F-line male turkey satellite cells from 48 h of proliferation (P) to 72 h of differentiation (D), **b** percentage of glypican-1-positive cells in RBC2 and F-line male turkey satellite cells from 48 h P to 72 h D, **c** percentage of syndecan-4-positive cells in RBC2 and F-line female turkey satellite cells from 48 h P to 72 h D, and **d** percentage of glypican-1-positive cells in RBC2 and F-line female turkey satellite cells from 48 h P to 72 h D. *Bars* represent the standard error of the mean. *Indicates a significant difference at $P < 0.05$

then maintained a constant level. In contrast, in the RBC2-line male turkey satellite cells the percentage of syndecan-4-positive cells decreased from 48 h of proliferation to 0 % at 72 h and 96 h of proliferation, and then at 72 h of differentiation reached 11 %. The percentage of glypican-1-positive cells in the F-line male was higher during proliferation, whereas the RBC2 glypican-1-expressing male satellite cells were higher during differentiation (Fig. 2b).

In comparing the syndecan-4-positive cells in the RBC2 and F-line female turkey satellite cells during proliferation and differentiation, both lines had similar trends. However, the F-line female satellite cells appeared to lag in their expression by 24 h compared to the RBC2-line female satellite cells (Fig. 2a). With regard to glypican-1, in the RBC2 female turkey satellite cells, the percentage of glypican-1-positive cells was higher than the F-line female turkey satellite cells during the proliferation stage and then switched during the differentiation stage (Fig. 2b). The trend of dynamic changes in the syndecan-4- and glypican-1-positive cells in the RBC2 and F-line female turkey satellite cells generally was the same.

Syndecan-4- and glypican-1-positive cell expression within the RBC2 and F-line female and male satellite cells

There were sex effects on the syndecan-4- and glypican-1-positive cells in both the RBC2 and F-line (Fig. 3). In RBC2 female satellite cells, syndecan-4 was expressed at a much higher level than in the male cells from 72 h of proliferation through 48 h of differentiation. At 48 h of proliferation the male cells had a higher level of syndecan-4-positive cells than the female cells (Fig. 3a). At 96 h of proliferation and 48 h of differentiation, RBC2-line female satellite cells contained about 30 % syndecan-4-positive cells compared to the male cells containing 0 to 2 % syndecan-4-positive cells. At 48 h of proliferation, RBC2-line male satellite cells had 16 % syndecan-4-positive cells, whereas females had 3 % syndecan-4-positive cells.

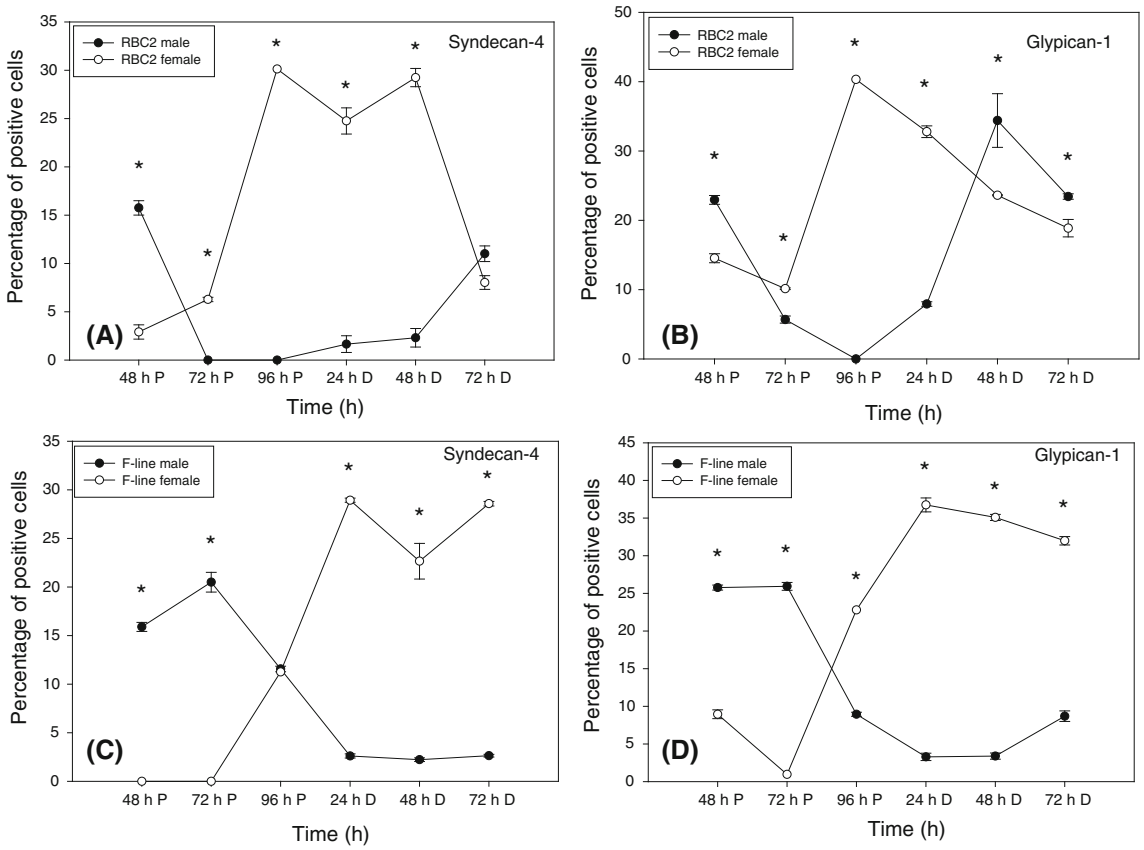

Fig. 3 Comparison of the percentage of syndecan-4- or glypican-1-positive cells in randombred control line 2 (RBC2) and 16-week body weight selected F-line male and female turkey satellite cells. **a** Percentage of syndecan-4-positive cells in RBC2 male and female turkey satellite cells from 48 h of proliferation (P) to 72 h of differentiation (D), **b** percentage of glypican-1-positive cells in RBC2 male and female turkey satellite cells from 48 h P to 72 h D, **c** percentage of syndecan-4-positive cells in F-line male and female turkey satellite cells from 48 h P to 72 h D, and **d** percentage of glypican-1-positive cells in F-line male and female turkey satellite cells from 48 h P to 72 h D. *Bars* represent the standard error of the mean. *Indicates a significant difference at $P < 0.05$

Male RBC2 satellite cells had higher levels of glypican-1-positive cells at the beginning of proliferation and the end of differentiation and lower levels during late proliferation and early differentiation (Fig. 3b). At 96 h of proliferation and 24 h of differentiation, the percentages of glypican-1-positive cells in the RBC2-line female and male satellite cells were 40 and 33 %, and 0 and 8 %, respectively. The male RBC2 satellite cells had 23, 34, and 23 % glypican-1-positive cells compared to the female cells having 15, 24, and 19 % at 48 h of proliferation, 48 and 72 h of differentiation, respectively. The expression of syndecan-4 and glypican-1 in F-line male and female turkey satellite cells were similar to the RBC2-line. Male F-line satellite cells had higher levels of both syndecan-4- and glypican-1-positive cells during proliferation and lower levels during differentiation (Fig. 3c, d). There were less than 3 % syndecan-4-positive cells in the F-line female cells at 48 and 72 h of proliferation and male cells at 24, 48, and 72 h of differentiation. At 48 h and 72 h of proliferation, F-line male satellite cells contained 16 and 20 % syndecan-4-positive cells, respectively, whereas during differentiation, the female cells contained 23 to 29 % of syndecan-4-positive cells (Fig. 3c). With regard to the glypican-1-positive cells, less than 10 % expressed glypican-1 at 48 and 72 h of proliferation in the F-line female cells and during differentiation in the F-line male cells (Fig. 3b). The percentage positive cells ranged from 23 to 37 % in the F-line female cells during differentiation, and the F-line male satellite cells at 48 and 72 h of proliferation had $\sim$26 % of the cells positive for glypican-1.

Discussion

Satellite cells are skeletal muscle stem cells that are responsible for postnatal or posthatch muscle growth and muscle regeneration. Growth selection has been shown to affect the proliferation and differentiation of satellite cells isolated from the same muscle. Velleman et al. [40] showed that the F-line male and female pectoralis major satellite cells when compared to the RBC2-line male and female pectoralis major satellite cells proliferated at a faster rate. During differentiation, the male F-line pectoralis major satellite cells had a higher level of differentiation. For the female pectoralis major satellite cells, the RBC2-line differentiated faster than the F-line. The increased rate of proliferation may be due to a prolonged period of proliferation in the growth selected F-line as supported by higher MyoD expression [43]. Summers and Medrano [44] demonstrated that high-growth mice have prolonged myoblast proliferation during embryonic development. These data suggest inherited differences in satellite cell potential for muscle growth.

Satellite cells are a heterogenous population of cells that express different genes including cell surface markers in both different muscles and the same muscle including the same muscle fiber [45]. Syndecan-4 and glypican-1 are cell surface heparan sulfate proteoglycans. They are expressed differentially by satellite cells. The proliferation and differentiation of satellite cells are regulated by both syndecan-4 and glypican-1 [33–39]. The expression of syndecan-4 and glypican-1 is precisely regulated with myogenesis. Syndecan-4 is highly expressed during turkey satellite cell proliferation and decreases with differentiation, whereas glypican-1 is expressed at high levels during differentiation and lower during proliferation [46]. Syndecan-4 primarily functions by mediating satellite cell migration [38] and glypican-1 by modulating fibroblast growth factor 2 (FGF2) binding to its receptor during differentiation [39, 47]. However, syndecan-4 is also capable of binding to FGF2 and regulating its signal transduction [48]. Fibroblast growth factor 2 is a potent stimulator of proliferation and an inhibitor of differentiation [49].

The effect of growth and sex on syndecan-4 and glypican-1 satellite cell populations is not known. It is likely that not all of the satellite cells express syndecan-4 or glypican-1. Therefore, the percentages of syndecan-4- and glypican-1-positive cells will likely change with the muscle development. In the current study, syndecan-4- and glypican-1-positive subpopulations in pectoralis major satellite cells were measured in vitro during proliferation and differentiation.

The percentage of syndecan-4-positive cells followed a similar trend in RBC2 and F-line male satellite cells except that the F-line cells maintained syndecan-4-expressing satellite cells for 48 h longer than the RBC2-line cells. A similar pattern also occurred in the RBC2 and F-line female cells. The F-line cells expressed syndecan-4 24 h longer than the RBC2-line cells. In regard to the percentage of glypican-1-positive cells, this was prolonged by 24 h in both the F-line male and female cells compared to the RBC2-line cells. This prolonged expression may provide the opportunity for increased proliferation and differentiation of the F-line satellite cells. Liu et al. [50] showed that the F-line satellite cells have higher FGF2 and FGF2 receptor 1 mRNA expression compared to the RBC2-line cells. Both syndecan-4 and glypican-1 can bind to FGF2 and regulate its binding to its receptor [48, 51]. It is possible that the prolonged expression of syndecan-4 and glypican-1 in the F-line may be associated with FGF2 signal transduction during proliferation and differentiation.

Within the RBC2 and F-lines, there are differences in the percentage of syndecan-4- and glypican-1-positive cells during proliferation and differentiation in the males and females. The percentages of syndecan-4- and glypican-1-positive cells were significantly lower in RBC2-line male

cells compared to the female cells. These differences do not reflect differences in proliferation and differentiation as these properties are unaffected between the sexes in the RBC2-line [40]. These data do suggest that sex differences exist in the male and female RBC2 satellite cells which could affect satellite cell function, but not limited to migration and the formation of multinucleated myotubes. In contrast to the RBC2-line, the F-line male satellite cells had higher levels of syndecan-4- and glypican-1-positive cells during proliferation and lower amounts during late differentiation. Since the F-line was selected for increased 16-week body weight, the increased levels of syndecan-4 and glypican-1 are likely associated with increased cell migration and modulation of FGF2 signal transduction leading to increased differentiation as the F-line male satellite cells differentiate at a higher rate than the female satellite cells but proliferation is not affected [40].

In summary, the percentage of syndecan-4- or glypican-1-positive satellite cells changes with development within and between different lines of turkey satellite cells and there are sex affects within each line of turkey satellite cells. Sex effects in satellite cells have been reported in other species affecting proliferation [52], but the results from the current study are the first to report growth and sex effects on satellite cell populations expressing syndecan-4 and glypican-1, and the dynamic nature of this expression during proliferation and differentiation. Future studies will need to address the functional significance of different satellite cell subpopulations with regard to muscle development, growth, and regeneration.

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